# The Oxford Handbook of Cultural Neuroscience

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*Editor in Chief* PETER E. NATHAN

# The Oxford Handbook of Cultural Neuroscience

*Edited by*

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Peter E. Nathan
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# ABOUT THE EDITORS

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Joan Y. Chiao is Director of the International Cultural Neuroscience Consortium, an international, interdisciplinary organization dedicated to advancing theory and methods in cultural neuroscience to address issues in culture and health. She received her Ph.D. in psychology from Harvard University and her B.S. with honors in symbolic systems from Stanford University. Her research is in social affective and cultural neuroscience, examining how race, culture, and social status affect the human mind, biology, and behavior. She serves on the editorial board of several journals, such as *Social Cognitive and Affective Neuroscience, Social Neuroscience, Journal of Personality and Social Psychology*, and *Culture and Brain*. She receives grant support from the National Science Foundation, National Institutes of Health, and the Japan Society for Promotion of Science.

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## Robert (Bob) Turner

Robert (Bob) Turner has played a key role in the invention of actively shielded gradient coils used widely in MRI; the development of diffusion-weighted imaging of human brain, which allows assessment of brain connectivity and evaluation of stroke damage; and the discovery of functional MRI by measurement of the effects of blood oxygenation changes. As a Max Planck Institute Director in Leipzig, Germany, he was engaged in the discovery of native cortical anatomical maps of individual living human brains using ultra-high-field MRI. He has published more than 220 scientific papers in a broad range of disciplines, and he is currently Director Emeritus of the Neurophysics Department at the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig (see http://www.cbs.mpg.de/staff/turner-10649), where he leads a major program of investigation into the functional anatomy of the human brain using ultra-high-field strength MRI. He is also Honorary Professor at the universities of Amsterdam and Nottingham.

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*The Oxford Handbook of Cultural Neuroscience* represents the first collection of scholarly contributions from the International Cultural Neuroscience Consortium (ICNC), an interdisciplinary group of scholars from epidemiology, anthropology, psychology, neuroscience, genetics, and psychiatry dedicated to advancing an understanding of culture and health using theory and methods from cultural neuroscience. The *Handbook* is intended to introduce future generations of scholars to foundations in cultural neuroscience and population health disparities, and to equip them to address the grand challenges in global mental health in the twenty-first century.

The volume editors would like to thank Dr. Bill Elwood (NIMH) for his programmatic support of ICNC scholars. We recognize the early career research accomplishments of ICNC Student Travel Awardees including Brandon Ng (University of Virginia), Desiree Phua (Nanyang Technological University), Yi Huang (South China Normal University), Yang Qu (University of Illinois, Urbana-Champaign), Alexandria West (York University), and Xiao-Fei Yang (University of Southern California). We warmly thank Brian Lai, Alissa Mrazek, Narun (Non) Pornpattananangkul, and Vernon Smith for their assistance with conference organization; Kylah Eagan, Tomeka Bolar, and Patricia Reese for their administrative support; and Mark Schurgin for his technical assistance. We thank the Cells to Society Program at Northwestern University's Institute for Policy Research for their co-sponsorship with the National Institutes of Health OppNet Program. We are grateful to the editors from Oxford University Press for their editorial guidance.

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# CONTENTS

# INTRODUCTION

Cultural neuroscience is a research field that has made notable theoretical and empirical advances in the cultural and biological sciences within the past decade. Scholars from anthropology, psychology, neuroscience, and genetics have collaboratively and independently gained novel insights into the mutual constitution of culture and biology. Research in cultural neuroscience addresses fundamental questions such as "where does human diversity come from?" and "how are culturally patterned behaviors and beliefs reflected in patterns of neural function?" By investigating how culture and genes co-shape the human brain and behavior, cultural neuroscientists are discovering both generalizable and culturally specific mechanisms of the mind, brain, and behavior. Empirical progress in cultural neuroscience can contribute to research efforts that address questions at the intersections of culture and health, including those related to the etiologies of population health disparities.

## Cultural Neuroscience and Health: Closing the Gap in Population Health Disparities

Notable developments within the field of cultural neuroscience have contributed to the formulation of the *Oxford Handbook of Cultural Neuroscience*. In 2011, the National Institutes of Health OppNet Program led by Dr. Bill Elwood funded the development of an International Cultural Neuroscience Consortium (ICNC). Founded in 2011 by Dr. Joan Chiao (Northwestern University) and Dr. Shinobu Kitayama (University of Michigan), the goal of the ICNC is to create and sustain an international, interdisciplinary community of scientists working on the acceleration, expansion, and strengthening of the scope of investigation in the field of cultural neuroscience. A second goal of the ICNC is to provide a research infrastructure for teams of scientists to address questions central to culture and health, particularly global mental health and population health disparities, with theory and methods from cultural neuroscience.

One of the specific aims of the ICNC is to host international conferences that bring together interdisciplinary scholars to address research theory and methods in cultural neuroscience and health. The first conference held in 2013 at the Hilton Orrington and Northwestern University in Evanston, Illinois was organized by Dr. Edith Chen (Northwestern University), Dr. Joan Chiao (Northwestern University), Dr. Shu-Chen Li (Technische Universitaet Dresden), Dr. Rebecca Seligman (Northwestern University), and Dr. Robert Turner (Max Planck Institute for Neurophysics). The theme of the three-day meeting was "Cultural Neuroscience and Health: Closing the Gap in Population Health Disparities."

Highlights from the scientific program include the Keynote Lecture of Dr. Pamela Collins (NIMH) "Crossing Borders for Mental Health: Global Cooperation in Research" and the evening lecture of Dr. Robert Turner (Max Planck Institute for Neurophysics) on "Brain and Culture: The Mutual Bootstrap." The contributions in this *Handbook* reflect the scholarly work of contributors at the conference and future directions regarding an agenda for research and pedagogy at the intersection of cultural neuroscience and health.

## Organization of the *Handbook*

*The Oxford Handbook of Cultural Neuroscience* is a scholarly collection of twenty-three chapters organized into seven parts. The chapters provide a comprehensive overview of research approaches in cultural neuroscience and population mental health.

Part I introduces the conceptual and methodological issues in cultural neuroscience. Seligman, Choudhury, and Kirmayer (Chapter 1) review the theoretical and methodological bases of current cultural neuroscience research and outline how cultural neuroscience research can contribute to the agenda of social determinants of health by embracing a more nuanced concept of culture. In Chapter 2, Northoff suggests that the processes underlying "enculturation of brain" and the cultural dependence of brain activity. Downey (Chapter 3) uses the case study of human echolocation as an example of the role that cultural neuroscience and neuroanthropology can play in characterizing the extraordinary range of human neurodiversity. Whitehead (Chapter 4) reviews the role of the culture-ready brain in development and evolution. In Chapter 5, Tobler and Christopoulos propose a theoretical and methodological framework of computational cultural neuroscience as an approach to explaining dynamic cultural phenomena.

Parts II–V consist of reviews of theoretical and empirical advances in cultural neuroscience. In Part II, four chapters review empirical and conceptual study of the cultural neuroscience of emotion. Iidaka and Harada (Chapter 6) report empirical investigation of how cultural values modulate emotional processing in the human amygdala. Nomura (Chapter 7) introduces a novel research agenda integrating genetic and cultural approaches to the study of serotonergic neural pathways in Japan. Immordino-Yang (Chapter 8) proposes the examination of embodiment and the social mind within the cultural neuroscience study of social emotion. Stein, Chiao, and van Honk (Chapter 9) address the promise and pitfalls of a cultural neuroscience approach to the study of health in South Africa.

In Part III, three chapters explain approaches to research on the cultural neuroscience of cognition. Gutchess and Huff (Chapter 10) review theory of holistic-analytic cognition and its relevance for neurobiological systems of memory and healthy aging. Stevenson, Bruce, Dwosh, Beattie, and Illes (Chapter 11) uncover the concept of dementia and wellness in a First Nation community and ethical considerations in cross-cultural community research. Demorest and Morrison (Chapter 12) propose the "cultural distance hypothesis of melodic expectancy" and implications of this hypothesis for quantification of culture.

In Part IV, three chapters survey advances in the cultural neuroscience study of social cognition. Han and Ma (Chapter 13) review how culture shapes neurobiological basis of the self. Telzer, Fuligni, and Galvan (Chapter 14) articulate the importance of family obligation as a cultural resource for Latinos. De Gelder, and Huis In't Veld (Chapter 15) review cultural differences in body language and its relevance for understanding cultural variation in the social brain.

In Part V, three chapters review cultural neuroscience research on intergroup processes. Harris, Capestany, and Tan (Chapter 16) theorize how next generation technologies can facilitate ecologically-valid study of health across cultures and species. Cheon and Hong (Chapter 17) conceptualize the cultural neuroscientific study of intergroup processes, including the discovery of gene-environment interaction in intergroup relations. Chiao and Mathur (Chapter 18) provide an overview of conceptual and empirical approaches to the cultural neuroscience study of pain and empathy.

Part VI on culture and genetics provides a cutting-edge review of advances in understanding how culture and genes affect health. Sasaki, LeClair, West, and Kim (Chapter 19) introduce the gene-culture interaction framework for health contexts. Morris and Connelly (Chapter 20) propose a novel epigenetic approach to the neuroscientific study of social behavior. Chen, Moyzis, Chen, and Dong (Chapter 21) advance the notion of the "enculturated genome" in cultural neuroscience research and its foundational role in population mental health.

Part VII discusses the rationale for closing the gap in population mental health disparities and the promise of cultural neuroscience to fulfill this goal. Yang and Benson (Chapter 22) lead this section with a comprehensive review of the role of culture in population mental health disparities. Maselko (Chapter 23) expands the discussion of how culture influences socioemotional development and concludes with potential implications of cultural neuroscience for understanding mental health disorder.

In the twenty-first century, mental health disorders comprise more than 10% of the global burden of disease. Yet the lack of effective preventative interventions and treatments worldwide suggests an urgent need for investment and prioritization of resources to study the etiology of global mental health. Conditions of unequal access to and distribution of resources within and across nations challenge national and international goals for achieving universal standards of human health. Cultural neuroscience represents a novel method through which scientists and public policy experts may discover and create culturally-competent interventions for illness prevention and treatment. By understanding how culture, genes, and the environment shape mechanisms of mind, brain, and behavior, we gain greater insight into the etiology, prevention, and treatment of mental health disorders across the globe.

Joan Y. Chiao
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## PART 1

# Conceptual and Methodological Issues in Cultural Neuroscience

CHAPTER

1

# Locating Culture in the Brain and in the World: From Social Categories to the Ecology of Mind

Rebecca Seligman, Suparna Choudhury, *and* Laurence J. Kirmayer

## Abstract

Cultural neuroscience explores the interplay between the social transmission of knowledge and the functional organization of the nervous system. However, much current cultural neuroscience simplifies culture into categories and constructs. The operationalization of culture as categories and traits that can be measured using questionnaires or priming techniques often lacks cultural validity. Moreover, treatment of culture as a set of fixed and even hard-wired traits has the potential to reify and essentialize differences between groups that are better understood as culturally constructed, fluid, and context-dependent. We argue that culture is better conceived of in terms of interactional processes rather than categories and demonstrate how a more nuanced understanding of culture in cultural neuroscience can contribute to an understanding of mind, self, and emotion as embodied, socially embedded, and situated or enacted in specific contexts, opening up new directions for research with greater potential relevance to issues of health and social disparity.

**Key Words:** Culture concept, cultural validity, ecology of mind, social categories, social determinants of health

## Introduction

Explanations that situate brain and cognitive function within the social and cultural environment of the person are increasingly called for from within neuroscience and psychiatry in order to develop multilevel theories of disease and their etiologies (Kendler, 2008; Van Os, Kenis, & Rutten, 2010). Advances in epigenetics have been especially influential in fuelling major shifts in scientific thinking about the relationship between the body and its environment (Labonté et al., 2012; McGowan, 2013; Szyf, 2013). Research on epigenetics has begun to reveal how interactions between the genome and the environment during the course of development lead to tissue-specific structural changes in, for example, the DNA methylation patterns that regulate cellular function. There is compelling evidence, for example, that early parenting experiences and social adversity alter the regulation of stress response systems for the life of the organism (Fish et al., 2004; McGowan et al., 2009; St. Sauver et al., 2004; Weaver et al., 2005). Such studies provide biological evidence that lived experience, developmental histories, dynamic interactions, and cultural contexts are all fundamentally bound up with biological processes as "low level" as gene expression.

In parallel to these developments in genetics, social and cultural neuroscience have become the most rapidly developing areas of cognitive neuroscience. While social neuroscience explores the role of the brain in social interaction processes, cultural neuroscience investigates how brain function correlates with cultural variation in a range of psychological processes, such as empathy and perspective-taking (Chiao & Immordino-Yang, 2013; Han et al., 2013). These research fields aim to operationalize social and cultural contexts of the person in the laboratory and to contribute material (embodied, neuronal, and functional) levels of description to theoretical accounts of "the social/cultural" (Chiao, 2009). In doing so, they posit that the human brain is fundamentally a social brain, adapted for social learning, interaction, and the transmission of culture (Emery, Clayton, & Frith, 2010; Frith & Frith, 2010; Rizzolatti & Craighero, 2004). Moreover, the brain's structural malleability is understood to be experience-dependent and long-lasting. For cognitive neuroscientists, evidence of genomic and neural plasticity and the acknowledgment of the social and cultural contexts of the person in these fields is a welcome shift. Rather than eliding differences in psychologies and their neural instantiations, cultural neuroscience puts at its focus these differences. For social science and humanities scholars, social and cultural neuroscience at first sight, offer a new twist to debates about the longstanding opposition between nature and culture (Fox Keller, 2009).

As a discipline devoted to investigating the brain in cultural context, cultural neuroscience in particular represents a corrective to universalizing trends in neuroscience. Whereas mainstream neuroscience often assumes the universality of its findings, cultural neuroscience highlights the idea that cultural and social environments may be a source of variability in the functional architecture and activity of the brain. Cultural neuroscience thus uses the tools of neuroscience—a rich set of rapidly developing methods—to conduct research that takes seriously the notion that human brains are highly responsive to cultural input. Because they allow collection of real-time data on neural function, such techniques represent potent tools for understanding how brains become encultured (Downey, Lende, & Brains, 2012). In addition, the techniques of neuroscience currently have immense rhetorical potency within both scientific and popular contexts as sources of evidence (Dumit, 2000; Poldrack & Wagner, 2008). As such, cultural neuroscience has the potential to produce findings that not only resist but also actively work against pervasive forms of biological reductionism (Kirmayer & Gold, 2012).

In addition to its potential to broadly reinforce contemporary understandings of the plasticity of human biological systems, cultural neuroscience also has the potential to truly advance our knowledge of how mind, self, and emotion emerge from the interaction of culture and brain. Such advances can open up new directions for research with greater relevance to issues of health and social disparity. However, in order to realize this potential, cultural neuroscience must bring together equally robust theory and method in both of the areas concerned. That is, in addition to cutting-edge tools from neuroscience, it must also bring cutting-edge tools for conceptualizing and measuring culture. Simplistic formulations of culture will not only fail to advance knowledge but when combined with the persuasive powers of neuroscience—with its great potential to influence scientific and popular thought—could actually promote harmful ideas about the nature of cultural difference.

The risk for harm is a central concern within an increasing number of critiques aimed at cultural neuroscience from scholars outside the discipline. Broad criticisms have been leveled at the assumptions built into many cultural neuroscience studies, at the failure to address certain kinds of research questions, and at the kinds of interpretations offered for many findings (Choudhury & Kirmayer, 2009; Denkhaus & Bös, 2012; Martinez Mateo, 2012; Seligman & Brown, 2010). In particular, critics have raised concerns about the potential for cultural neuroscience to actually contribute to forms of essentialism and biological reductionism (Denkhaus & Bös, 2012; Martinez Mateo, Cabanis, Stenmanns, & Krach, 2013). Studies linking particular groups of people to particular forms of brain function, critics argue, run the risk of promoting simplistic ideas about the nature of these differences, suggesting implicitly that they are somehow fixed or immutable characteristics of individuals. Application of such formulations to questions of health disparity in particular could do more harm than good because they can easily be interpreted as evidence of the intractability of such disparities or used in the service of victim blaming.

Experiments investigating differences in cognitive processing between cultural groups, largely dependent on functional neuroimaging as a methodology, have proliferated in recent years, but interpreting these data to understand how social and cultural worlds interact with brain structure and function, and how these in turn produce symptoms psychiatrists recognize as mental disorder, continues to be problematic. Despite attempts to objectify cultural differences or culturally shaped processes through experimental paradigms, measurements, and comparisons, the experimental space itself—from the task design to interpretation—is pervaded by contingencies and choices, and the categories and concepts are shaped by the wider culture in which they are studied (Daston & Galison, 2007).

In a recent and especially pointed critique of cultural neuroscience published in the journal *Frontiers in Human Neuroscience*, Martinez Mateo et al. (2013) argue that the leap in cultural neuroscience from characterizing cultural differences in "psychological" tendencies to the treatment of such differences as *biological* has not been sufficiently problematized. However, although the use of biological evidence to reinforce notions of cultural difference can be problematic, the idea that cultural and social factors influence not only peoples' psychologies but also their bodies is worth retaining. This idea has become increasingly important within cultural anthropology where the term "embodiment" is used to refer to the various ways in which culture is inscribed on human bodies. In particular, anthropologists think about embodiment as the process by which cultural practices, political–economic conditions, and power relations affect bodily experiences and, through a process of implicit, experiential learning, come to shape peoples' bodies (Bourdieu, 1977; Csordas, 1990; Seligman, 2014).

The notion of embodiment has become central to the way in which anthropologists conceive of culture itself. In fact, contemporary anthropological understandings of culture almost uniformly include the idea that the practices and enactments that are central to culture fundamentally shape and are shaped by human bodies. Yet these notions of culture emphasize the complex and dynamic nature of the interchange between individuals, their bodies, and cultural contexts. From this perspective, the way that specific individuals internalize, engage with, resist, manipulate, and *embody* cultural influences is variable, and it depends on numerous factors, including interactions among social position (e.g., gender, socioeconomic status, and age), social context, and personal history.

Thus, a more complex notion of culture and of culture–individual interaction necessarily leads to a more complex understanding of how culture is embodied, including how brains may be shaped developmentally and entrained by cultural influences. Adding complexity to the way that culture is conceptualized in cultural neuroscience research can therefore help us avoid the pitfalls of essentialism and reductionism while facilitating the ability to build theory with broad relevance. A more complex vision of culture will also allow cultural neuroscience to contribute research with greater real-world applicability to issues of health and social disparity. Our goal in this chapter is to help introduce such an understanding of culture into the field. Our primary focus is therefore on culture rather than on the brain.

We begin with an overview of the way in which culture has typically been conceptualized and operationalized in cultural neuroscience research, and we discuss problems of cultural validity in current research paradigms that hinder the applicability of findings to research on health disparities. We offer a more complex vision of culture and describe the implications of such an understanding for studies of culture–individual and culture–brain dynamics. We conclude by describing how a critical approach within cultural neuroscience, which understands the brain as fundamentally "situated," can contribute to research on health disparities.

## Culture in Cultural Neuroscience Research

What do researchers in the field of cultural neuroscience mean when they talk about culture and how is culture typically studied in cultural neuroscience research? Because published research in the field often does not include explicit definition of what is meant by culture, both of these questions are best answered through an examination of the way in which culture is represented and measured within these studies (Denkhaus & Bös, 2012). To date, most studies that fall under the heading of cultural neuroscience uniformly use functional magnetic resonance imaging (fMRI), and to a lesser extent event-related potential (ERP) technology, genetic, and neurohormonal markers, in the context of experimental study designs in laboratory settings. The constraints of the methodology (e.g., the scanning environment of MRI) often mean that the operationalization of social and cultural processes is necessarily thin, a proxy chosen to represent something much more complex. For example, the reaction time taken by a research subject to choose between two cartoon faces on a screen in a brain scanner is taken to reflect the subject's preference for, or prejudice against, a person in a real-life scenario. As such, mainstream approaches have been criticized for their tendency to inappropriately reduce complex social phenomena to "variables" and to conceptualize culture as mere "factors" that "modulate" cognition (Choudhury & Kirmayer, 2009; Martinez Matteo, Cabanis, Cruz de Echeverría Loebell, & Krach, 2011; Roepstorff, 2013).

Studies in cultural neuroscience are most often designed to look for "cultural" differences in the neural correlates of cognitive processes, and both cognition and culture are modeled in ways that are amenable to experimental manipulation. Thus, cognitive processes are most often measured with the use of isolated cognitive tasks, and culture is frequently modeled through group comparisons. The groups that are assembled in cultural neuroscience research often reflect everyday categories of ethnicity. In the United States, for example, these have been configured in terms of very heterogeneous categories used in the national census: African American, American Indian and Alaska Native, Asian American, Latino, and White. These categories do not work well in other countries because they reflect the distinctive history and demography of the United States and include complex distinctions along lines of language, ethnicity, and racialized identities. Internationally, the groups compared in cultural neuroscience typically reflect broad geographic categories, which ignore enormous internal diversity in terms of both ethnicity and other important cultural dimensions of identity and experience.

It is extremely common, for example, for cross-national comparisons to be used to represent culture; that is, comparison of Danish or American subjects to Chinese or Japanese subjects represents the cultural variable at work in many studies. Moreover, comparisons of participants from different nations often serve as a proxy for a broader contrast between what are understood to be two large, divergent cultural groups—the East Asian or "Eastern" and the Euro-American or "Western" cultures. Because people from multiple nations are seen to fall into these two broad cultural categories, a study comparing Japanese and American subjects and one comparing Danish and Chinese are both ultimately understood to reveal broad differences between members of Eastern and Western cultures. This approach is imported from a long tradition of cross-national comparisons in cross-cultural psychology that has produced a variety of measures of cultural difference and some robust findings (Heine & Ruby, 2010; Kitayama & Uskul, 2011; Nisbett, 2003; Triandis, 1995).

What is most remarkable about the use of this East/West comparison is the degree to which it has come to stand for culture in the field as a whole. In a review of the literature by prominent cultural neuroscientists (Han & Northoff, 2008), out of 50[1] original cultural neuroscience studies cited in the text, all but 2 compared participants from East Asian versus European countries. Similarly, all 30 of the original research articles discussed in a recent overview of the literature by scholars outside the field (Denkhaus & Bös, 2012)[2] used the East Asian versus Euro-American comparison.[3]

The pervasiveness of the East/West dichotomy has had important implications for the way in which culture is conceptualized in cultural neuroscience as a whole. First, although there is some acknowledgment from researchers within the field that "Eastern" and "Western" do not represent homogeneous cultural groups (Han & Northoff, 2008), heavy use of this broad comparison has acted to obscure cultural complexity in many studies by smoothing over differences across and within the groups of people compared. Reduction of complexity, in turn, has facilitated the conceptualization of culture in rather narrow terms, as broad differences in ideologies and norms operating at the group level.

In fact, reliance on the East/West rubric has led to an almost exclusive focus on a specific limited set of norms and ideologies, which are thought to differ across these two broad cultural groups. In particular, there has been intense attention to differences in what is known as "self-construal," or whether people tend to hold more collectivistic/interdependent or individualistic/independent orientations toward self and others. Preference for these two orientations is understood to fall out along East/West lines, with people from "Eastern" cultures on average expressing more collectivistic/interdependent attitudes and those from "Western" cultures oriented more toward individualism/independence. As discussed further later in the chapter, from an anthropological perspective, the vision of culture created by the focus on differences in these broad norms is one that is deceptively static and uniform.

To give a sense of the pervasiveness of the self-construal construct within cultural neuroscience, a full two-thirds of the 30 studies examined in a review of the literature used it as part of their research (Denkhaus & Bös, 2012). Such intense attention to this construct has likely resulted in part from practical concerns. The construct, which

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[1] There are many other studies cited in this text, but we count approximately 50 original studies that fall under the heading of cultural neuroscience.

[2] The authors of the review selected articles that were cited by other articles within the cultural neuroscience literature, based on the premise that these articles could be considered particularly relevant within the field.

[3] There was a small amount of overlap between the two reviews: They included eight of the same studies.

is drawn from classic research in cross-cultural psychology (Markus & Kitayama, 1991), is associated with a robust literature demonstrating correlations among self-construal, country of origin, and numerous other cognitive processes, including what is known as "holistic" versus "analytic" cognition (Gutchess & Park, 2006; Nisbett, 2003; Nisbett, Peng, Choi, & Norenzayan, 2001). Moreover, user-friendly research instruments for measuring self-construal style have been well validated and are widely available (Singelis, 1994). Hence, the existing theoretical and methodological infrastructure make this construct easy to build hypotheses around, easy to apply, and easy to justify.

However, it is also likely that overdependence on this construct has reinforced reliance on the East/West rubric, feeding the tendency to focus exclusively on research subjects who fall into these broad cultural categories. In other words, it seems probable that lack of analogous constructs around which Latin American, Middle Eastern, or South Asian "cultures" can be easily compared is one reason why there has been virtually no cultural neuroscience research conducted among, for example, Mexican, Moroccan, or Pakistani participants. The absence of such a widely accepted construct representing a cultural trait that is easily compared across groups may make designing studies among these populations seem more challenging.

Intentionally or not, however, the narrow focus on a particular set of questions and participants communicates something about the kinds of cultural phenomena that are meaningful and of interest. For instance, design of studies around the East/West, interdependent/independent dichotomies communicates the idea that studying culture is about identifying *differences* between groups of people (Denkhaus & Bös, 2012). In effect, only certain facets of culture are singled out for comparison simply because they reflect salient differences between the broad groups being compared. In addition, the characterization of these facets or dimensions is based on the perspective of the dominant or tacitly normative group (in this case, Euro-Americans). The dimensions of culture that are interesting might look very different from other perspectives. Moreover, some critics have argued that studies devoted to establishing differences between the *particular* groups of people almost always compared in cultural neuroscience research invoke both orientalist and Eurocentric worldviews by comparing Asian "others" to a normative Euro-American standard (Martinez Mateo et al., 2013). Thus, in addition to the potential political implications of this "culture as difference" paradigm, its implicit messages have also had a conservative effect on the kinds of studies that get designed and on the shared vision of culture operating within the field.

The way in which the self-construal construct is operationalized has also helped shape how culture is conceptualized within the field. Individualistic versus collectivistic orientations are typically modeled as discrete traits that can be measured in the laboratory with the use of questionnaires. Statistical differences between groups in terms of self-construal are then correlated with differences in neural function associated with the performance of specific cognitive tasks. Thus, the "culture" variable in many studies consists of group-level difference in response to such questionnaires (Ray et al., 2010; Singelis, 1994). This way of modeling culture suggests that it is conceptualized as (1) something that exists primarily in individuals; (2) something that is similar across all individuals in a given cultural, ethnic, or geographic group; and (3) something that is present and expressed in a form that is relatively fixed and impervious to context. In other words, this way of operationalizing culture assumes that peoples' self-reported orientations on a questionnaire filled out in the laboratory accurately represent their relationship to the norms and values of their culture and, moreover, that an individual's relationship to the norms and values of the culture is equivalent to culture itself.

Thus, on the one hand, use of questionnaires to measure culture is problematic in the sense that it effectively reduces culture to a set of mental traits. On the other hand, compared to the representation of culture simply in terms of membership in a national or ethnic group, use of questionnaires to measure cultural traits is preferable in the sense that it opens up the possibility of measuring intragroup variability. This is important because, as cultural neuroscientists have noted, "Eastern" and "Western" are far from homogeneous cultural groups (Han & Northoff, 2008). Thus, although representatives of these two groups may differ on average in terms of their performance on self-construal questionnaires, there will inevitably be variability within, and overlap between, groups.

A study by Tetsuya Idaka (see Chapter 6, this volume), for instance, shows significant variability within a sample of Japanese participants in terms of interdependent versus independent orientation, and these differences are associated with differences in amygdalar activation in response to an unpleasant image (see similar results in Ma et al., 2013).

These findings underscore the facts that (1) within ethnic or national groups there are differences in the kind of ideological orientation represented by the self-construal construct, such that some Japanese may look more like some Americans in terms of self-construal and vice versa,[4] and (2) variability within ethnic or national groups along such dimensions may be associated with social and cultural factors that are more salient than membership in these broad cultural groups. Investigation of what such factors might be will require the development of new research paradigms.

A relatively recent addition to the methodological toolkit for measuring culture in cultural neuroscience, the use of what is known as "cultural priming," seems to move in the direction of investigating how such norms and values are made salient for individuals. In particular, priming paradigms, which are designed to evoke specific cultural orientations among study participants through the use of cues or stimuli, seem to embrace the premise that contextual factors may activate certain kinds of normative orientations within individuals (Hong, 2009). In other words, culture is represented not as fixed traits within individuals but as skills and dispositions to respond in particular ways to specific contexts, which the culturally shaped social world provides.

However, many of these studies use cues associated with broad national identities, such as the American flag, to prime cultural identity (Hong, Benet-Martínez, Chiu, & Morris, 2000). This suggests that they are operating within the same cross-national comparison paradigm seen in many other cultural neuroscience studies. Other priming studies have used variables such as focus on different pronouns (i.e., "I" vs. "we") as cues to prime individualism/collectivism (Oyserman & Lee, 2007, 2008). Hence, although the priming approach has the potential to add substantial complexity to the way culture is conceptualized by acknowledging that variability in normative orientations may exist not only within groups but also within *individuals*, studies using this design have thus far mostly defaulted to the same set of norms and ideologies used to represent culture in most cultural neuroscience research. The challenge is how to bring more realistic social contexts into the laboratory and allow individuals to respond in ways that reflect cultural processes or strategies.

In summary, the vision of culture communicated through its operationalization in cultural neuroscience research is currently a rather narrow one that views culture as sets of broad norms and values operating at the level of national or ethnic identity. However, as shown in the following section, culture exists not only in peoples' heads but also in the world, where it is dynamically enacted and embodied by and between individuals in particular situations and contexts.

## Culture in Anthropology

The concept of culture is central to the field of anthropology, and yet there has never been a single, agreed upon definition of culture within the field. This is at least in part because anthropologists have come to understand culture as too complex and dynamic to define in simple terms. Anthropologists understand culture, on the one hand, as a system of shared knowledge that exists within peoples' minds. On the other hand, culture is understood to be constituted by peoples' behaviors, enactments, and interactions. Hence, from this perspective, culture has a dual life—within peoples' minds and out in the world. As we have already discussed, in the cultural neuroscience literature, culture is treated almost exclusively as norms and values located inside peoples' heads.[5] Although most anthropologists would agree that values and norms (along with beliefs, meanings, and dispositions) are central elements of culture, they would emphasize that these elements take the form not only of ideas but also of *actions*—often referred to within anthropology as "praxis" (Ortner, 1984, 2006)—and *discourse*, or the way in which language is mobilized and made to "do" something in the world (Foucault, 1971; Knorr-Cetina, 1981; Latour & Woolgar, 1986).

In fact, there is a growing consensus within anthropology that ideas (knowledge and beliefs) and actions (discourse or praxis) are equally important. It has become increasingly clear, moreover, that the two do not always exist in a one-to-one relationship with one another. That is, behaviors do not always match beliefs and beliefs do not always

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[4] Anthropologists have long known this to be the case, but a study by a group of cross-cultural psychologists (Na et al., 2010) empirically demonstrates differences between group-level ideologies and individual attitudes. However, to date, these ideas have not found their way into most cultural neuroscience research.

[5] When described explicitly, culture is typically discussed in terms of "values, beliefs, and practices" (Cheon & Hong, Chapter 17, this volume; Chiao, 2009; Han & Northoff, 2008).

match behaviors, but both are fundamental for our understanding of culture. In addition, the areas in which the two diverge are particularly rich domains for investigating how cultures work. Although the knowledge and action that make up cultures are collective—that is, they are shared among and constituted by a group of people—these elements of culture are also not uniformly distributed. The knowledge and behaviors of members of the same culture are largely overlapping, but they also diverge in important ways and along meaningful individual and social lines. Moreover, the relationship between knowledge and behavior may differ across individuals and social groups. Individuals and groups may behave differently but still draw on largely overlapping beliefs and values, and vice versa. In the cultural neuroscience literature, such differences are elided by the large-scale group comparisons employed by most studies.

Crucial to understanding the dualities of culture[6]—its life both in minds and in the world, its collective and individual qualities—is the notion that cultural knowledge and enactments are situated, contextual, and contingent. This means that the particular knowledge and behavior sets that are drawn upon by an individual at any given time are a function of cues and constraints within the social and/or physical environment. Individuals hold vast amounts of cultural knowledge, some of it implicit, some explicit, some rarely accessed, some used all the time, and even some that is conflicting and contradictory. Just as environmental factors may turn on or activate particular genes (Zhang & Meaney, 2010), elements of context such as social role, interpersonal relationships, and social constraints help activate certain sets of cultural knowledge. These same elements determine whether and how individuals will *act* in relation to such situated knowledge. Moreover, just as "genes" are not discrete units with a fixed function but, rather, elements of a more complex dynamic network that regulates the transcription and translation of information encoded in DNA, so too cultural knowledge must be understood not as isolated bits but as part of dynamic systems of social action and regulation that include other people, discourses, and institutions.

Research by anthropologist Douglas Hollan (1992) on cross-cultural differences in the self exemplifies many of these features of culture. Hollan's work among bereaved American undergraduates and the Toraja people of Indonesia demonstrates that independent and interdependent norms and values may be held and acted upon by individuals from both societies, even though one or the other ideology is dominant in each. For example, Hollan demonstrates that most of the bereaved students in his study subscribe to a dominant American ideology of selfhood in which autonomy, individual strength, and self-control are highly valued. For many, these values were activated by the experience of loss and served as the core elements guiding their response to bereavement. However, this research also demonstrated that experiencing the death of a loved one triggered the opposite value for some students, leading them to express a sense of interconnectedness with loved ones and a sense that their own selves were defined at least in part by their relationships to others. One student said, for instance, "You're stripped of a certain role [when someone dies]. One of the people you relate with is gone. And so that side of you is gone."

Similarly, Hollan's (1992) work among the Toraja suggests a dynamic in which multiple beliefs and values may compete for saliency depending on the situation. Torajans are quintessentially "interdependent" in their orientations; nevertheless, Hollan demonstrates that Torajans think about and enact degrees of self-interest in certain contexts and under particular conditions. For example, despite the fact that Torajans highly value cooperation, compliance, and helping others, many of them also expressed in interviews that they could not be forced to do anything they did not want to do. Moreover, at times, Torajans actively resisted having to cooperate or assist others, despite the fact that they strongly endorse these values, by avoiding the person or people by whom these calls were made. Both examples from Hollan's work underscore the situated and contextual nature of cultural norms and values and also the often imperfect fit between belief and behavior.

Other anthropologists have demonstrated the importance of *social status* in determining the relationship between norms and values and behaviors. Claudia Strauss (1992) has shown that although working-class men in the United States endorse the "American dream" value of pulling oneself up by one's bootstraps to achieve success, the men she worked with were behaviorally motivated not by this value but by a different one having to do with the need to provide for their families. Adrie Kusserow (2004) has similarly shown that the dominant

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[6] See Dominguez Duque, Turner, Lewis, and Egan (2010) for a complementary discussion of culture's dualities in relation to cultural neuroscience research.

American ideology of individualism is understood and enacted very differently depending on the social class to which individuals belong. Kusserow argues that individualism is actually a huge symbolic category subsuming many different meanings that different individuals and social groups may take up and manipulate in ways that fit their specific needs.

Kusserow's (2004) analysis draws our attention to another key element of cultural complexity: the issue of meaning. Individual idiosyncrasies, life experiences, and social position shape how specific people respond to, engage with, incorporate, resist, and manipulate cultural materials. Considering meaning helps us understand how such culture–individual dynamics work. For example, independence means something different to a recently bereaved American college student than it does to one who has not suffered such a loss, and it means something different still to a student who has suffered multiple losses. Similarly, the idea of "success" means something different to working-class American men than it does to upper-middle-class ones. The kinds of cues and contexts that trigger knowledge about "success" will therefore differ for individuals in these two groups, as will the kinds of behaviors directed toward the goal of "success." Meaning thus mediates many of the cultural processes we have been discussing.

Moreover, research by anthropologists has demonstrated that understanding the work of meaning in cultural systems can help reveal hidden dynamics related to health and health disparities. Dressler, Grell, and Viteri (1995) have shown, for instance, that the meaningfulness or salience of cultural knowledge can directly affect peoples' health. Dressler et al.'s research in Jamaica revealed a relationship between social status and norms related to success similar to the relationship demonstrated in Strauss' (1992) study of working-class American men. He showed that although Jamaicans from lower-, middle-, and upper-class status all had similar models of success, individuals varied in their ability to behave in accordance with these models. Particularly striking was the finding that not behaving in a way that was consonant with this cultural ideology had negative health effects in the form of higher blood pressure, but only for members of the middle class.

Meaning thus has a dual role in these dynamics. First, these findings demonstrate that a mismatch between cultural knowledge and behavior can negatively affect health via stress pathways, but only when the cultural knowledge in question is truly salient for an individual or social group because it taps into self-relevant meanings. Second, certain kinds of social and economic constraints become particularly meaningful when they act as obstacles to the ability to enact cultural knowledge. This work thus highlights how the complex interactions among things like social status, social constraint, and culture–individual dynamics are often mediated by meaning.

Anthropological research has also demonstrated how recognizing the role of meaning in culture–individual dynamics can contribute to our understanding not only of pathways relevant to health disparity but also of pathways of resilience. Multiple studies have demonstrated how shared cultural meanings can serve as individual and group resources, allowing people to use such meanings in the service of their specific needs and goals (Kirmayer, 2005; Kirmayer et al., 2011). Anthropologist Peter Stromberg uses the metaphor of a "symbolic smorgasbord" to describe this phenomenon, noting that "any society offers its members a panorama of symbolic resources" onto which individuals may "map the idiosyncrasies of their experience" (Stromberg, 1985, p. 57).

In his influential analysis of Sri Lankan religious ecstatics, Gananath Obeyesekere (1981) demonstrates how women with histories of stressful and traumatic experiences (i.e., family conflict, miscarriage, death of loved ones, unhappy or abusive marriages, etc.) use available religious symbols from a form of Hindu devotionalism in order to express and resolve their own emotional distress and conflict. Obeyesekere's analysis of the way in which these women adopt and enact certain religious symbols and practices, growing huge matted dreadlocks and behaving as priestesses, demonstrates the therapeutic potential of translating personal distress into culturally intelligible terms. This analysis thus provides a model for understanding why religious belief and behavior are often associated with better physical and mental health and, more broadly, for understanding the importance of both social forces and idiosyncratic experiences in shaping culture–individual dynamics.

Although the ecstatics in Obeyesekere's (1981) study represent a particularly extreme case of self-transformation through religious devotion, many less extraordinary examples of the use of cultural symbols and meanings to make sense of personal experience can be found in both religious and nonreligious contexts. Numerous scholars have demonstrated how spirit possession, a phenomenon found in 74% of the 488 societies sampled in one study (Bourguignon, 1973), offers an opportunity for individuals to communicate self-related meanings through the use of religious discourses and practices (Boddy, 1989; Kapferer, 1979; Lambek, 1993; Mendenhall et al., 2010). Others have demonstrated similar processes in the context of Christian conversion narratives, in which individuals are able to use the language of Evangelical Christianity to help resolve emotional conflicts (Stromberg, 1993). These processes are also visible in medical contexts, in which people use the discourses and meanings associated with medical and psychiatric categories and illness etiologies to make sense of their own experiences of suffering (Becker, 1997; Cain, 1991; Kirmayer, 2000; Kleinman, 1988). The idiom of trauma has become a particularly powerful cultural symbol that individuals can tap into in an effort to reinterpret events and emotional responses in terms that are salient to themselves and others (Kidron, 2003; Seligman & Kirmayer, 2008; Young, 1997).

These observations also underscore another essential characteristic of cultural systems: They are dynamic and interactive, not fixed and stable. As previously discussed, individuals respond to and interact with cultural materials and contexts in a variety of ways, but culture is also responsive to and even constituted by the ways in which individuals enact it. In other words, the direction of influence is not always from culture to individual; rather, belief and behavior at the individual or subgroup level feed back to influence the shape of cultural systems in a process that can be thought of as a more embodied form of what the philosopher Ian Hacking (1999) calls “looping.” Such looping processes extend beyond the reinforcement of cultural concepts to include the social constitution of context itself, when the practices, bodily dispositions, and habits of individuals and subgroups act to shape and reinforce larger cultural systems (Bourdieu, 1977; Seligman, 2014).

An example of the way such looping processes operate comes from our own research on cross-cultural experiences of dissociation. The term *dissociation* refers to a category of experience in which elements of self-conscious awareness, including memory, perception, and identity, become dis-integrated. In Euro-American contexts, such experiences are often understood as symptoms of psychiatric disorder. Findings from our research suggest that such pathological meanings are most often attached to dissociative experiences in contexts in which there is high emphasis on unitary and coherent forms of selfhood (Seligman & Kirmayer, 2008). Because such experiences violate normative expectations, individuals who have them come to occupy a category of people with mental disorders. This shapes their experiences, contributing to distress, and their identities, as people who are sick. In addition, pathologization of such experiences further reinforces their non-normative status. Thus, a looping process takes place among cultural norms and values and personal experiences and meanings.

However, our research also suggests that in some cultural contexts, such as that of the spirit possession religion studied by the first author in Brazil, there is less emphasis on unitary selfhood. In the context of this religious culture, in which the shared ontology includes spirits and other beings who can occupy human selves, dissociative experiences are not pathologized. Instead, such experiences are attributed to spirit possession, and those who have them often become socially and spiritually empowered as religious adepts. By drawing attention to the role of cultural ideologies of selfhood in distinguishing between pathological and nonpathological forms of dissociation, these findings underscore the idea that meanings and attributions affect experience, and peoples’ experiences loop back to shape and reinforce meanings, attributions, and ultimately cultural systems.

It is worth noting that the concept of looping is relevant to cultural neuroscience not only as a model for how to think about the dynamic and interactive nature of cultural systems but also because cultural neuroscience research may become part of such cultural looping processes. Contemporary reliance on scientific expert knowledge in defining self and personhood, in the United States in particular (Dumit, 2000; Hacking, 1998; Rose, 1990, 1998, 2007), means that popular dissemination of findings from cultural neuroscience (e.g., see the 2010 *Newsweek* article by well-known science writer Sharon Begley) contributes to the creation and reinforcement of shared cultural meanings and, by extension, helps create kinds of people, identities, selves, and experiences (Martinez Mateo et al., 2013). For instance, the idea that independence is ingrained in Americans at the neural level may contribute to and/or reinforce the fashioning of selves in the United States for whom independence and self-interest become even more explicit values (Dumit, 2000).

Figure 1.1 presents a model of such culture–individual dynamics, visually depicting the multidirectional influences that exist among cultural norms

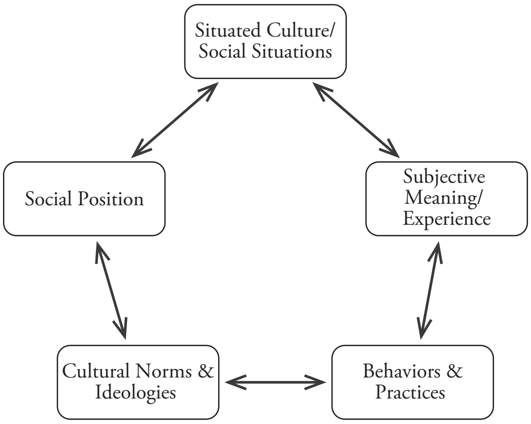

**Figure 1.1** Dynamics of Culture–Individual Interactions. The diagram depicts the complex and dynamic interactions between individuals and their cultures, which are mediated by multidirectional influences among norms and ideologies, social positionality (i.e., social role and status), specific social situations and situated cultural knowledge, subjective meaning and experience, and behaviors and practices.

and ideologies, social positionality (i.e., social role and status), social situations/situated cultural knowledge, subjective meaning and experience, and behaviors and practices. Importantly, the figure can be read from any point and in either direction, highlighting the idea that individuals draw from their repertoire of cultural norms and ideologies, based on their social location and the particular nature of the social situation, to construct meaning and guide behaviors and practices; but equally, behaviors and practices affect individual experience and the meaning that individuals make of any given social situation, and therefore what cultural norms and ideologies are assembled or drawn upon in that moment (Latour, 2005). Figure 1.1 thus captures both the dynamism of looping processes and the situated and contextual nature of culture–individual interactions.

## Locating the Brain in the Social World

Thus far, our discussion has emphasized the importance of culture–individual interactions, but it has not had much to say about culture–brain interactions. Returning to the example of our work on dissociation offers an opportunity to demonstrate how the role of the brain might be conceptualized in relation to the kinds of dynamic processes we have described. Evidence from neuroimaging studies of pathological dissociation demonstrates that alterations in consciousness that fall under this heading are often correlated with cortical inhibition of the amygdala and other subcortical areas (Sierra & Berrios, 1998). These studies thus suggest that experiences characterized by the fragmentation of self-conscious awareness may be associated with the failure to attend to, process, and integrate certain streams of information at the cortical level.

Whether such patterns of neural activity are the same in both spiritual and pathological forms of dissociation is a question that has not been empirically investigated. However, a looping model suggests that dissociative experiences of *all* kinds are likely to be the products of mutual feedback processes in which patterns of attention and information processing create experiences that must be explained by cultural scripts, and cultural scripts and social imperatives, in turn, influence the allocation of attention and information processing resources—possibly through the activation of cortical inhibitory mechanisms (Seligman & Kirmayer, 2008). Ultimately, knowing where and how neural function fits into this looping process tells us far more than simply mapping the neural function.

Moreover, this way of conceptualizing the interactions of neural mechanisms with cultural ones may serve as an important model for thinking about the role of culture–brain interactions in other forms of psychopathology as well. In particular, locating patterns of neural activation within larger looping processes that include the action of meanings, attributions, social identities, and experiences helps us see that the difference between pathological and nonpathological states is not defined by the presence or absence of neurophysiological dysfunction alone. Cultural neuroscience research that models the complexity of culture–brain interactions more successfully can thus contribute to nonreductionist approaches in health research that resist the tendency to treat the brain as the ultimate cause of pathology and thus reflect a more sophisticated understanding of the cultural ecology of mind.

Further illuminating the methodological and conceptual challenges of the experimental process in cultural neuroscience research, and in the interpretation of data (Choudhury & Slaby, 2012), is also a crucial step to developing a nuanced ecology of mind. Recognizing the relevance of cognitive and neural mechanisms for behavior and psychiatric symptoms, but taking the embeddedness of the brain seriously, a "critical neuroscience" approach espouses a view of a "situated brain" (Choudhury & Gold, 2011). This view demands wider exploration of the way in which brain function has to be investigated in the context of an organism's environment (Kirmayer, 2006; Lock, 1995). The brain and nervous system, no less than the mind, are *situated*, which requires an approach that blurs the distinction between nature and culture. Such an approach departs from mainstream cultural and social neuroscience by challenging the ontological primacy of the brain in investigating and understanding the mind. It also maintains room to examine the interaction of scientific culture with the object of study—for example, the categorization of research subjects, definitions of the "social" and "cultural," and categorization of disease, which is contingent on the culture of neuroscience.

In other words, a critical neuroscience approach integrates research on the looping effects involved in dynamic and situated culture–brain interactions with the study of the looping effects involved in the production and consumption of neuroscientific knowledge. Slaby and Choudhury (2012) propose four ways in which experimental research practiced within a critical neuroscience framework can contribute to a complex theory of mind that includes multiple realms of description and acknowledges the co-constitutive relationship between them (Slaby & Choudhury, 2012, p. 43):

1. Demonstration of alternative possibilities of results of neuroscience experiments by modifying technical parameters or comparing and re(de)fining categories
2. Exploring routes to empirically investigate social and cultural phenomena without assuming universal neural mechanisms from the outset
3. Enriching behavioral theories by allowing for pluralistic viewpoints and methodologies to result in layered explanations of complex phenomena
4. Examining the subtle relationship and feedback loops between popular opinion or ideologies about the brain and findings in neuroscience

A critical approach based on these principles can serve the goal of opening up interpretive possibilities that are more relevant to answering the questions cultural neuroscience has recently set out to investigate concerning health disparities.

## The Cultural Shaping of Social Determinants of Mental Health

In this section, we illustrate some of the ways that a more critically oriented cultural neuroscience can shed light on social determinants of health, using examples drawn from indigenous peoples whose experiences of historical trauma and ongoing structural violence have evident effects on their mental health and well-being.

Broadly speaking, social determinants of health refer to all of the social factors, including social structure, institutions and practices, identities, and interpersonal processes, that impact on health (Marmot, 2007; Marmot & Wilkinson, 2006). Among the most powerful social determinants are poverty, inequality, and social exclusion. Culture intersects with these social determinants in several ways: (1) by defining the social categories and identities to which people are assigned; (2) by attaching specific meaning and consequences to these identities; (3) by shaping the ways that individuals and groups respond to their social identities and positions; and (4) by normalizing social arrangements—that is, by making them seem like natural or necessary conditions. Often, this normalization results in the cultural assumptions underlying such social arrangements becoming taken-for-granted or invisible to participants. Cultural comparison and critique is therefore necessary to make the tacit dimensions of the social world visible.

The study of the mental health of indigenous peoples serves to illustrate the ways in which culture shapes notions of self, personhood, and the subsequent experience and response to other social determinants of mental health (Kirmayer & Valaskakis, 2009). In North America, indigenous peoples flourished for thousands of years before contact with Europeans. They formed very diverse cultural traditions with different languages and ways of life. Some were nomadic hunters, others established agricultural communities or large empires with complex hierarchical social structure. With colonization, they were enclosed within new societies dominated by the values and ways of life of the European societies. The common elements across these diverse traditions therefore represent not so much shared cultural values, traits, or identities as the shared predicament of coping with colonization, marginalization, and deliberate efforts to suppress indigenous cultures, languages, and traditions (King, Smith, & Gracey, 2009). The health consequences of this history have been profound, with many groups experiencing elevated rates of suicide, substance abuse, and common mental disorders (Reading, 2009; Reading & Wien, 2009).

In recent years, there has been increasing recognition of the links between current mental health and social problems in indigenous communities and the history of colonization, marginalization, and bureaucratic control by the nation state. In Canada, the historical system of government-mandated Indian residential schools has been singled out as a major factor in the continuing problems faced by Aboriginal communities. The Indian residential schools explicitly aimed to extinguish the culture of indigenous peoples. They did this by taking young children far from their homes and communities and confining them to education institutions that systematically excluded and denigrated any knowledge or expression of indigenous languages and cultures. The schools also exposed children to harsh, punitive environments with high levels of physical and sexual abuse. Individuals who eventually returned to their communities and went on to become parents were profoundly affected by these experiences of trauma and abuse and by the institutional models of disciplining and adult authority. The resultant difficulties in childrearing thus impacted on the next generation. Moreover, because whole cohorts of children in particular communities were subjected to the residential school system, its effects extend beyond individuals to include changes in the dynamics of entire families and communities.

The impact of these policies across generations has been traced by historical and qualitative health research (Brant Castellano, Archibald, & DeGagné, 2008). More recently, quantitative studies have confirmed these observations. For example, a survey of a representative sample of almost 3000 First Nations adults in Manitoba found that experience of abuse in residential school was associated with suicide attempts among adults; moreover, exposure of a parent or grandparent to abuse in residential school was associated with suicidality among adults who did not attend residential school themselves (Elias et al., 2012). There is also evidence that the more generations in a family that attended Indian residential schools, the greater the psychological distress among the younger generation (Bombay, Matheson, & Anisman, 2013). However, the impact of adversity varies with social context and developmental stage, and the modes of transmission across generations are affected by childrearing practices as well as family, neighborhood, community, and other aspects of the social environment.

The mediation of these transgenerational effects is therefore likely to be very complex (Gone, 2013). Figure 1.2 illustrates some of the ways in which the experience of residential school may lead to transgenerational transmission of mental health problems. Conventional trauma theory emphasizes transgenerational transmission of effects through psychological processes involving cognition and emotion that influence childrearing (Hinton & Kirmayer, 2013). Thus, a parent who has experienced violence and privation may be preoccupied and emotionally unavailable, or labile and reactive, to a child, thus increasing the risk of mood or affective disorders in the child. When the parent's behavior is abusive, this may cause trauma-related symptoms in the child, and although the traumatic experiences of the child are quite different from those that the parent endured, the overall framing of the experience as "historical trauma" may lead some to emphasize similarities and the causal arc. However, the Canadian residential school policy had much broader impact than the marks it left on individuals, constituting a sustained attack on the health of indigenous peoples at the levels of family, community, and nation. Moreover, beyond this specific historical trajectory, the broader history of colonization and oppressive social policies has resulted in ongoing situations of social exclusion and marginalization that constitute forms of structural violence.

Culture plays a role in these transgenerational effects and ongoing adversity in many ways, including (1) influencing childrearing practices; (2) configuring family structure and process; (3) promoting particular individual, interpersonal, or collective strategies for coping, resilience, and recovery; (4) shaping the community response to adversity; and (5) locating collective identity in relation to a larger society that confers a stigmatized and devalued status on indigenous people and exposes them to racism, discrimination, and disempowerment (Kirmayer et al., 2007). In other words, culture here resides in the ways that Aboriginal peoples understand themselves, the places they live, the forms of community and subsistence activities in which they participate, the bureaucratic and political institutions they must negotiate, as well as underlying concepts of self and personhood that are rooted in particular ontologies (Kirmayer et al., 2011). These dimensions of culture, in turn, all take on specific meaning and health consequences in the context of the larger society that either valorizes or devalues indigenous identity and experience (Waldram, 2008). The experiences of grief, anger, and demoralization associated with historical loss and ongoing marginalization can be measured in part through self-report (Whitbeck, Adams, Hoyt, & Chen, 2004). These experiences are not only internalized but also situated, evoked by particular settings. Thus, in considering the role of culture in social determinants of health, it is essential to consider not just the culture of the minority

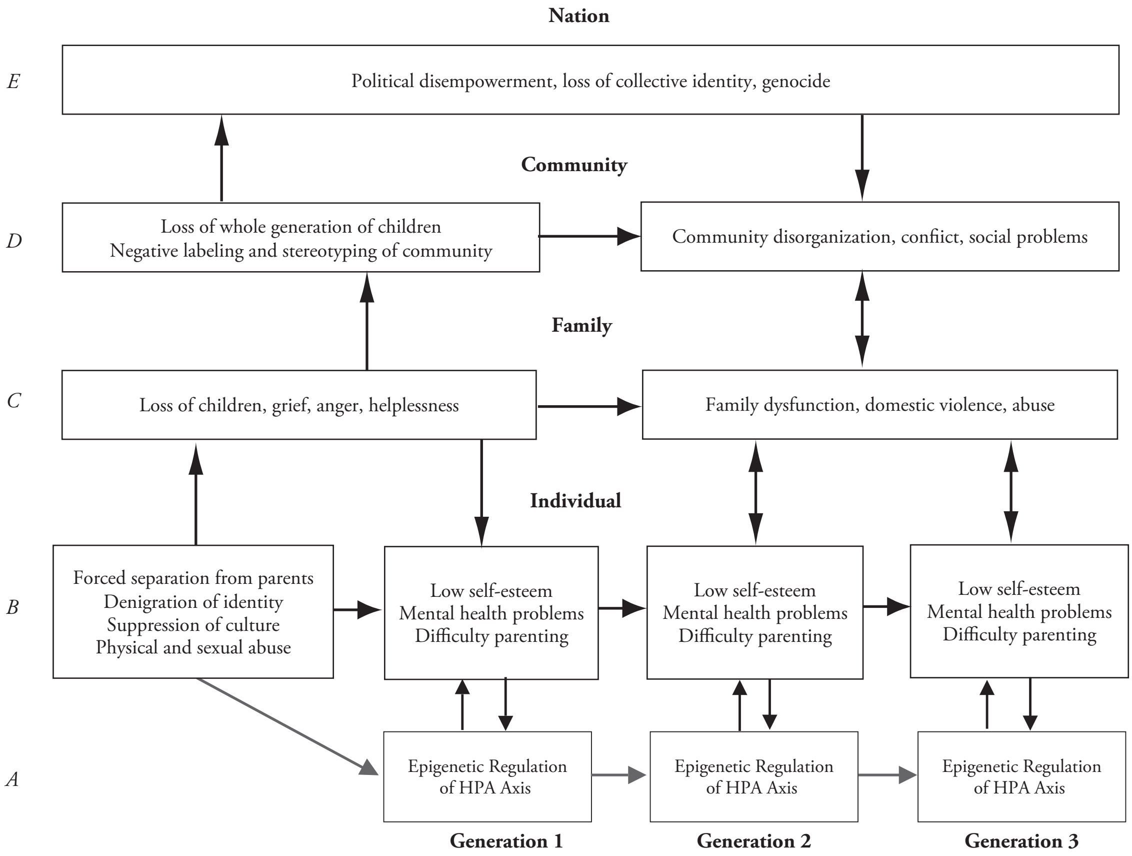

**Figure 1.2** Transgenerational Transmission of Historical Loss and Trauma. The diagram depicts some of the interacting pathways through which the effects of violence, trauma, and privation may be transmitted across generations. Individuals exposed to the residential school system endured early childhood separation from family, suppression and denigration of language and culture, and physical and sexual abuse. These events have effects at multiple levels, including (A) epigenetic processes of the altered regulation of hypothalamic–pituitary–adrenal stress response system; (B) individual's cultural identity, self-esteem, and efficacy; (C) disorganization of families by forced separation and the importation of parenting models influenced by experiences in institutions; (D) disruption of communities through the loss of whole cohorts of children; and (E) political disempowerment and marginalization of whole nations or peoples. In addition to residential schools, many other policies and practices operated at different levels to reinforce the negative effects on health and well-being.

Adapted from Kirmayer et al., 2007.

group but also the larger matrix of social practices, institutions, and values in which individuals and groups are embedded. Culture is made and has its most obvious consequences at the interface between different groups or segments of society.

Recent work on epigenetics and the regulation of stress response systems suggests another way in which effects of violence, loss, and conflict may be transmitted across generations (McGowan et al., 2009). Such work suggests that childhood abuse and adversity may alter hypothalamic–pituitary–adrenal (HPA) axis regulation and affect mental health outcomes in part through differential expression of hippocampal glucocorticoid receptors (McGowan et al., 2009). The possible epigenetic transmission of some consequences of trauma and violence across generations is certainly of potential relevance to understanding these enduring effects, but it represents just one strand or level of a complex process that includes many other neurobiological and sociocultural dimensions. The impact of life events on the regulation of the HPA axis and other regulatory systems will play out in contexts largely defined by the higher levels—hence, cultural neuroscience research on such topics must build on basic neurobiological studies of effects of stress, trauma, and loss to consider how these are modulated by contexts with varying levels of social support and access to culturally relevant coping mechanisms. The story of neuroplasticity and, indeed, of the epigenetic modifiability of the functional genome points toward the ongoing effects of social circumstances as well as deliberate adaptive strategies in healing and recovery.

For indigenous peoples, such strategies may be uniquely tied to their relationship with the land and the ability or inability to engage in traditional land-based practices. Although much cross-cultural research has examined the differences between individualistic and collectivistic orientations, work with indigenous peoples highlights another dimension of variability in notions of personhood across cultures. In particular, many indigenous peoples living in remote communities, engaged in close interactions with the land and natural environment, might be characterized as having an "ecocentric" sense of self and personhood in which the living environment, including the landscape, animals, and other natural forces, is in constant intimate transaction with the individual (Kirmayer, Fletcher, & Watt, 2008). Ways of thinking and being, as well as the concept of health, are tied to specific contexts, landscapes, and types of activity.

This points to distinct ways of experiencing self in relation to the environment that should be possible to study in field research or laboratory studies with analogs to the natural environment. Just as configurations of the self have been shown to differ across cultures, with people from more collectivistic or sociocentric backgrounds showing patterns of information processing in particular tasks (or in the resting state) that differ from those from individualistic backgrounds, so might we expect corresponding differences in paradigms designed to examine the ecocentric self. For the ecocentric self, attacks on the land may be experienced as attacks on the self with direct implications for well-being. Aspects of this orientation should be demonstrable in experimental settings.

In addition to the physical environment, people from diverse cultures, including some indigenous peoples, may participate in ontologies in which there is an invisible or spirit word, peopled by the spirits of ancestors (Ingold, 2004; Kirmayer, 2007). Maintaining harmonious relationships with this invisible world is also important for the health and well-being of individuals and communities. The notion that the social world includes invisible persons or non-human beings may have reflections in the organization of self and other in cognition, and this may be measurable in laboratory paradigms that examine experiences of volition (Deeley et al., 2013). Such work may have implications for our understanding of social processes of identity, connectedness, and belonging that are important contributors to health and mediators of social support shaped by cultural concepts of personhood and configurations of the social world.

Finally, for contemporary indigenous peoples, some of the most salient issues related to health and well-being concern the social and political contexts in which they live. In a widely influential study, Chandler and Lalonde (1998, 2008; see also Chandler, 2010) showed a clear association between the level of local control, cultural continuity, and self-determination of a community and important indicators of health, including the rates of death by suicide, accidents, and high school completion. To shed light on how such community-level indicators contribute to individual and collective well-being, cultural neuroscience would need to adopt a research program that explores the processes that indigenous peoples recognize as central to their well-being and endurance, including connection to land, cultural and linguistic retention and revitalization, and political activism.

Ultimately, examining stress responses and coping in real-life settings or ecologically meaningful experimental analogs has the potential to shed light on how the historical past and present interact for individuals to give rise to emotional states, cognitive orientations, and patterns of psychophysiological responding that are deleterious to health or that represent effective strategies for dealing with historical trauma and loss.

## Conclusion

Cultural neuroscience can contribute to the agenda of social determinants of health in several ways. It can allow us to understand some of the underpinnings of the diversity of experience of individuals. It can shed light on the nature of gene–brain–environment interactions by revealing culturally influenced pathways and mechanisms. Neuroscience holds the promise of providing measures of underlying processes that do not depend on self-report and hence can add substantially to our understanding of how self-awareness and narration interact with bodily processes. Developmental neuroscience can reveal modes of plasticity and response to learning and life experience that can explain pathology and open up avenues for intervention.

To realize this promise, cultural neuroscience needs to develop methodological approaches that capture the realities of culture. Specifically, it is essential to distinguish culture(s) from the categories it constitutes, such as race and ethnicity. Although aspects of culture can be decomposed as bundles of correlated traits, factors, roles, skills, or tasks, cultures also form integrated systems. Hence, cultural constructs, including race and ethnicity, must be understood as *situated*—that is, as contextually determined, embodied, and enacted in ways that involve not only individuals but also, necessarily, dyads and larger social groups and systems. Recognizing the dynamic nature of culture would suggest the importance of devising measures of the impact of changing contexts, tasks, expectations, agency, and social positioning. A systemic view would allow us to draw from our understanding of subsystems and small-scale causal models to reconstitute culture as systems of meaning and practice engaged by individuals with identifiable goals, strategies, and constraints. This would also involve tracing the consequences of cultural constructs—like those generated by cultural neuroscience research—from the social world through the laboratory and back.

At the same time, the enthusiasm for neurobiological explanations for complex behaviors poses particular risks for efforts to understand and address the social determinants of health. Some of these risks stem from the limitations of current experimental paradigms. The way that experimental groups are identified using common sense or popular categories of ethnic, racial, or cultural identity contributes to reifying these social categories, obscuring their social origins and serving to naturalize them. The need to isolate variables in experiments to identify simple, linear causal pathways may obscure the fact that most biological phenomena are embedded in systems with dense networks of mutual influence or circular causality. Some forms of pathology may stem from the dynamics of these systems and may not be recognized in the simplified models that are amenable to study in the laboratory. The focus on the brain tends to reinforce the tendency in psychology to study individuals rather than interacting dyads or larger groups or systems. Hence, in such paradigms, vulnerability and resilience are located within the individual rather than social relations and systems. Most critically, the exclusive focus on neurobiological levels of explanation may divert attention, resources, and political will from tackling the social and economic problems and structures of disadvantage that are both proximate and ultimate causes of many forms of ill health (Mooney, 2012). Indeed, we must be alert to the potential abuses of cultural neuroscience to reinforce stereotypes and rationalize inequalities. Properly conceived, cultural neuroscience can deepen our understanding of human diversity and our nature as cultural beings and contribute to a dynamic view of health and well-being as rooted in the ways that individuals make creative use of the resources and constraints of culture, context, and community.

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## CHAPTER 2

# Cultural Neuroscience and Neurophilosophy: Does the Neural Code Allow for the Brain's Enculturation?

George Northoff

## Abstract

Many studies show the cultural dependence of the brain's neural activity, but the underlying mechanisms of such "enculturation of brain" are unclear. How it is possible for the neural activity to be so strongly dependent on and shaped by the cultural context? Conceptually, this raises the question for the concept of culture and its relationship to the brain and what exactly is meant by "enculturation of brain." Empirically, the enculturation of brain raises the more general and basic question of how stimuli and their respective cultural context are encoded into neural activity. I suggest a statistically based coding strategy that encodes the stimuli's statistical frequency distribution rather than the single stimuli into neural activity. The cultural dependence of neural activity may be traced back to the brain's neural code and its particular encoding strategy, the encoding of the stimuli's natural and sociocultural statistics, which may account for the enculturation of brain.

**Key Words:** cultural neuroscience, neurophilosophy, context dependence, encoding, natural statistics, sociocultural statistics, "enculturation of brain, " embrainment of culture, layers of culture, psychiatry

## Introduction

### *Why Cultural Neuroscience?*

Neuroscience and culture? Recent research has shown that cultural differences strongly impact the brain's neural activity. The same stimuli are perceived differently by subjects in different cultures. And the same tasks such as decision-making are performed differently and recruit different regions and/or degrees of neural activity (for a review, see Han et al., 2013). Despite all the results and progress in the recently formed discipline of cultural neuroscience, we do not really know why and how the brain and its neural activity are so sensitive to cultural differences.

Given our current knowledge about the brain, one would expect that brains from subjects in different cultures react more or less uniformly to the same stimuli or tasks. We currently assume that different regions and networks in the brain process particular stimuli or tasks. It starts with the sensory regions, continues with the motor regions, and ends with the higher-order cortical regions such as the prefrontal cortex that are associated with different cognitive functions. Despite such presumably clear and straightforward association between functions and regions/networks, we nevertheless observe cultural differences.

Let us explicate what exactly is at stake here. The same stimuli or tasks are apparently processed in different ways by subjects from different cultures. Also, the same regions/networks are recruited and used in different ways by subjects from different cultures. The processing of stimuli/tasks as well as the recruitment of regions/networks thus seem to be strongly dependent on the social and specifically the cultural context. This has led authors such as Kitayama to assume reciprocal loops between brain and cultural context reflecting what can also be described as "enculturation of brain" (Han et al., 2013; Kitayama & Park, 2010; Kitayama & Uskul, 2011).

How is such context dependence as enculturation of brain of both the stimulus/task processing and the regions/networks' recruitment possible? We currently do not know. Although we have assembled plenty of data that show the cultural context dependence of different functions such as perception, language use, reasoning, and decision-making, we do not know why and how our brain's neural activity is apparently dependent on the respective cultural context.

What are the neural mechanisms in the brain that make possible the cultural context dependence of both task-evoked activity and region/network recruitment? Because the cultural context dependence can be observed across basically all different stimuli/tasks, functions, and regions/networks, it must be mediated by some kind of basic feature of the brain. This is where neurophilosophy comes in.

### *Why Neurophilosophy?*

What is neurophilosophy? The term *neurophilosophy* has been explicitly introduced by P. Churchland (1986) in her book with the same name in which she describes certain thematic convergences and overlaps between neuroscience and philosophy. One central topic is the relationship between mind and brain and how mental features such as self, free will, and consciousness are related to the brain and its neural activity. Neurophilosophy in the Anglo-American world reduces mental features to the brain: The brain's neural activity is considered not only a necessary but also a sufficient condition of mental features such as self and consciousness. Obviously, this leaves no space for culture, unless reduced to the brain, for shaping mental features.

Nonreductive models of neurophilosophy, in contrast, presuppose a more complex relationship between mental and neural features (e.g., see Northoff, 2004, 2011, 2013a, 2013b, 2014). The brain's neural features are considered a necessary but not sufficient condition of mental features. Along with the brain and its neural activity, we need some additional factor, an extra ingredient to understand how the brain and its purely neuronal states bring forth mental states. What is this additional or extra ingredient? Cultural neuroscience tells us that it must be the cultural context that the brain seems to include in generating its neural activity that then is manifest in the processing of stimuli/tasks and recruitment of regions/networks.

How and in which way must the brain generate its neural activity such that it can become as dependent on the cultural context as we observe it in cultural neuroscience? Generation of neural activity touches upon a basic feature of the brain and its neural activity: How must the brain encode stimuli and tasks into its neural activity such that their respective cultural context is manifest in the brain's subsequent processing and region/network recruitment? This relates to the question of the brain's neural code, which is a central issue in especially nonreductive forms of neurophilosophy (Northoff, 2011, 2013a, 2013b, 2014).

### *The Aim and Sections of This Chapter*

The aim of this chapter is to address the question of cultural context dependence and thus enculturation of brain as a central issue in cultural neuroscience in light of recent neurophilosophical considerations about the brain's neural code. Specifically, I raise the question of how the brain must encode its neural activity in order to make possible the kind of cultural context dependence—that is, enculturation of brain—we observe in the neural processing of stimuli/tasks and the recruitment of the various regions and networks in the brain.

The chapter comprises six main sections. In the first section on cultural neuroscience, recent findings on the cultural context dependence of perception and self are briefly presented. This section serves only as a brief introduction providing paradigmatic examples while refraining from an exhaustive discussion of the various findings. This is complemented by the second section, in which the concept of culture and how it relates to the brain is discussed, including the enculturation of brain. The third section discusses the concept of encoding, which refers to how the brain generates and encodes its neural activity. That is followed by the fourth section, in which the encoding strategy of the brain is discussed in detail, focusing on "natural statistics." This is extended in the fifth section to the encoding of "sociocultural statistics," for which an example is given. Finally, the sixth section briefly discusses the implications of the brain's encoding of natural and sociocultural statistics for cultural neuroscience, neurophilosophy, and psychiatry.

I conclude that cultural neuroscience can be considered a paradigmatic model or example for the question of the brain's neural code, the encoding of stimuli or tasks into neural activity. Accordingly, I claim that neurophilosophy as well as neuroscience in general can benefit and learn very much from cultural neuroscience with regard to the question of the encoding of neural activity.

## Cultural Considerations: Cultural Context Dependence of the Brain's Neural Activity

### *Cultural Context Dependence of Neural Activity During Physical Stimuli—Perception*

How can we demonstrate the cultural context dependence of the brain's neural activity? From the many examples in recent cultural neuroscience, I briefly highlight two paradigmatic examples—perception and self. Perception is about physical features in the world, whereas the self concerns purely mental features. If both perception and self show cultural context dependence in more or less the same way, it hints upon some basic feature of the brain's neural activity prior to the distinction between physical and mental features.

Based on the assumption that Westerners attend to salient objects whereas East Asians are inclined to attend to a broad perceptual and conceptual field (Nisbett & Masuda, 2003; Nisbett, Peng, Choi, & Norenzayan, 2001), Jenkins, Yang, Goh, Hong, and Park (2010) tested whether the neural activity in the lateral occipital cortex to a target stimulus is more sensitive to background scenes in East Asians than in Westerners. They scanned American and Chinese participants during perception of pictures consisting of a focal object superimposed on a background scene that was congruent (e.g., a deer in the woods) or incongruent (e.g., a television in the desert) with the target object. The target object was presented on different novel scenes or on a single repeated scene on four successive trials. Adaptation magnitude was calculated by subtracting the neural activity to objects on a repeated scene from that to objects on different novel scenes.

Jenkins et al. (2010) found that the neural activity in both the right and the left lateral occipital cortex showed significantly greater adaptation to incongruent scenes than to congruent scenes, suggesting sensitivity of the occipital activity to the background scenes. However, this effect was evident in Chinese participants but not in American participants. Similar results were observed in another study that recorded event-related potentials (ERPs) to target objects that were presented on semantic congruent or incongruent background scenes (Goto, Ando, Huang, Yee, & Lewis, 2010). It was found that a negative ERP component peaking at approximately 400 ms after stimulus onset (N400), which has been shown to be sensitive to processing semantic relationships (Kutas & Hillyard, 1984), was enlarged by target objects presented on semantically incongruent versus congruent background scenes; this effect was observed in Asian Americans but not in European Americans.

### *Cultural Context Dependence of Neural Activity During Mental Stimuli—Self*

The previous example concerned physical stimuli to the sensory system and our perception of them. What about mental stimuli and thus inner mental experience such as a sense of self? Zhu, Zhang, Fan, and Han (2007) tested cultural differences in the neural activity underlying representation of personality traits of oneself and a close other. According to Markus and Kitayama (1991), Western cultures encourage self-identity that is independent of social contexts and others, whereas East Asian cultures emphasize fundamental social connections, leading to an interdependent view of the self and partial overlap in representation of the self and close others. This proposition may predict shared neural mechanisms of representation of the self and a close other in East Asian cultures but not in Western cultures.

To test this proposition, Zhu and colleagues (2007) scanned Chinese and Westerners using functional magnetic resonance imaging (fMRI) during trait judgments of oneself, a close other (i.e., one's mother), and a celebrity. They found that relative to trait judgments of a celebrity, trait judgments of oneself significantly activated the ventral region of the medial prefrontal cortex in both Chinese and Westerners, suggesting a similar neural substrate of representation of oneself in the two cultural groups. However, trait judgments of one's mother versus a celebrity activated the same brain region in Chinese but not in Westerners, suggesting shared neural representation of the self and a close other in Chinese but not in Westerners. This finding reveals a neural model of cross-cultural variations in representations of a close other in relation to the self. Hence, even something as mental as our sense of self seems to be subject to cultural dependence. This has been extended and further confirmed in other studies (for review, see Han et al., 2013).

## Conceptual Considerations: What Is Culture? Layers of Culture

### *"Location" of Culture*

#### WHAT IS CULTURE? LAYERS OF CULTURE

What is culture? This question is as general as it is difficult. Many researchers associate culture with ideas and specifically with explicitly held beliefs and values. That, however, is only what is visible on the surface. Going into deeper layers of culture, one encounters different, more implicit and tacit aspects. This is well observed by Durkheim, who noted that culture to humans may be analogous to what water is to fish. In the same way the water is always already there and essential for the fish to exist, culture is always already there and provides the context that makes it first and foremost possible for us to live.

How can we further explicate the implicit and tacit aspects of culture? Kitayama and Park (2010) distinguish between different layers or key constituents of culture. A first component is explicit values that are focused on and shared in a given cultural group. For example, independence and individualism are shared values among especially North American cultures. In contrast, collectivism and interdependence are the dominating and shared values in Asian cultures.

In addition to explicit values and beliefs, Kitayama and Park (2010) assume cultural tasks as the second key component. Cultural tasks include conventions, routines, rituals, or shared scripts for action. For instance, the value of independence is strongly reflected in certain tasks and actions, such as interpersonal debate, fierce competition, a focus on self-expression and self-esteem, and the booming industry of self-help guides. In contrast, interdependence is manifested in the desire for social harmony, filial piety, social consensus, and strong emphasis on groups.

Whereas cultural tasks can be situated at the border between implicit and explicit processing, Kitayama and Park (2010) assume yet a third key component of culture that remains completely implicit. They speak of implicit psychological and neural tendencies. Such psychological tendencies consist of, for instance, different types of perception holistic versus analytic, whereas neural tendencies surface, for instance, in the neural activity in the ventromedial prefrontal cortex in independent and interdependent selves (discussed previously). This third aspect that is completely implicit or tacit is the layer of culture that I target here because this layer is where culture and brain seem to be most intimately connected, and it is this intimate connection and how it is generated that is the topic of chapter.

## HOW ARE CULTURE AND BRAIN CONNECTED?

### *Brain-Reductive Approach*

How are culture and brain connected? The third key component in the three-layer model by Kitayama and Park (2010) introduces the brain. Kitayama describes this relationship between culture and brain using the terms "embrainment of culture" and "enculturation of brain" (Kitayama & Uskul, 2011). What is meant by "enculturation of brain" and "embrainment of culture"? The brain and its neural activity are shaped and constituted by the respective cultural context—this amounts to enculturation of brain. At the same time, the cultural context is shaped and constituted by the brain, leading to the embrainment of culture.

How can we further describe "embrainment of culture" and "enculturation of brain"? Depending on one's discipline, different approaches may be pursued. The psychologist may want to associate a different function with both: The embrainment of culture may be related to those cognitive and sensorimotor functions that underlie our explicitly held beliefs and values, whereas the enculturation of the brain may be associated with the different forms of learning, such as probabilistic learning. The neuroscientist may extend this by searching for the neural correlates underlying the respective psychological functions.

The guiding question for both psychological and neuroscientific approaches is the following: What are the psychological and neural mechanisms that underlie the beliefs, values, and cultural tasks? This differs from the approach of the anthropologist, who may rather describe the different forms in which both the encultured brain and especially the embrained culture are manifested in different cultures. He or she may thus focus on the beliefs, values, and especially the cultural tasks rather than on their underlying cognitive and sensorimotor functions. The guiding question here is thus: How do the beliefs, values, and cultural tasks look in different cultures?

What about the philosopher? He or she may question why and how there is such enculturation of brain and embrainment of culture. One could, for instance, imagine a world that is a purely logically possible world as distinguished from our actual natural world, without both encultured brain and embrained culture. Hence, the focus here is on the presuppositions of embrainment and enculturation rather than on the beliefs, values, and cultural tasks themselves. The guiding question here is, Why and how are embrainment and enculturation necessary and thus possible at all? How can we link that philosophical question to the brain? This is the task of the neurophilosopher. He can provide such a link in two different ways. He can first argue that the philosopher's question of the why and how of embrainment and enculturation is covered by the neuroscientific question—the search for the neural correlates of the psychological functions underlying the beliefs, values, and cultural tasks. In this case, he reduces beliefs, values, and cultural tasks and ultimately culture as whole to the brain. One may then want to speak of a brain-reduced approach to culture in particular and neurophilosophy in general.

*Brain-Based Approach*

Does such a brain-reduced approach really cover the complexity and different layers of culture? A brain-reduced approach may, if at all, apply to the upper and more explicit layers of culture, the beliefs and values (and possibly the cultural tasks) and their underlying sensorimotor and cognitive functions (including their neural correlates). In contrast, it falls short with regard to the lower, more implicit layers of culture—that is, implicit neural and psychological tendencies as described by Kitayama and Park (2010). Why? Those implicit neural and psychological processes, the third key component, can only be understood on the background of some intimate relationship between brain and culture. This intimate relationship between brain and culture has been expressed by different terms, including "culture–brain nexus" (Domingez Duque, Turner, Lewis, & Egan, 2010), "neuroculture interaction" (Kitayama & Uskul, 2011), and "encultured brain" (Choudary, 2010).

How can we characterize the intimate relationship between brain and culture in further detail? The intimate relationship between brain and culture seems to hold across different cultures so that it must be regarded as a universal feature of both brain and culture. "Universal" here means that it occurs across different cultures, as the anthropologist would say (Markus & Kitayama, 1991). Such universal feature must be distinguished from particular features that are bound to a particular culture such as the previously mentioned beliefs, values, and cultural tasks.

The philosopher, in contrast, may want to speak of necessity or necessary conditions; that is, the brain cannot avoid becoming encultured (it is thus necessarily rather than contingently encultured) in the same way culture cannot avoid becoming embrained. Although this sounds rather abstract, it becomes more concrete once we turn to neurophilosophy.

The neurophilosopher may want to say that such intimate and seemingly necessary connection between brain and culture may be related to the particular way in which the brain interacts with its respective context, the culture. Specifically, the neurophilosopher may want to investigate those neural mechanisms by means of which the brain encodes the cultural context into its neural activity as such. That in turn may be central for understanding why and how the neural activity during the various functions—sensorimotor, affective, cognitive, and social—is shaped by its respective cultural context.

How can we better illustrate the intimate relationship between brain and context? In the same way that water is necessary for fish to exist, the cultural context may be essential for the brain to generate its neural activity. In other words, the brain is strongly dependent on its context, the culture, for encoding and generating its neural activity that otherwise, in the absence of culture such as when reducing it to and locating in the brain, would remain impossible. Accordingly, instead of "locating" culture in the brain and thus presupposing a brain-reduced approach, we need to pursue a brain-based and culture-based approach to understand the enculturation of brain: Cultural context is a necessity for the brain to generate and encode its neural activity. Without cultural context, the brain could simply no longer generate its neural activity. Where can we then "locate" culture? Culture can no longer be exclusively located within and reduced to the brain but, rather, between brain and its context. Consequently, culture is as much in the brain as it is in the context of the brain; specifically, culture must be located or situated in the relation between context and brain because it is here where the brain's neural activity is generated and encoded. This implies that conceptually and methodologically we need to abandon the brain-reduced approach to culture and replace it. Accordingly, the neurophilosopher may better presuppose a brain-based rather than brain-reductive approach to the brain–culture relation because otherwise she may lose what she aims to investigate, namely culture and its intimate relationship with the brain.

## *Interaction Between Culture and Brain*

### HOW DO CULTURE AND BRAIN INTERACT?

*Brain and Its Neural Tendencies as Fourth Layer*

Previously, the model of culture by Kitayama and Park (2010) was introduced with the three key components—explicit values and beliefs, implicit–explicit cultural tasks, and implicit psychological and neural tendencies. Especially the latter, the implicit neural and psychological tendencies, seem to presuppose an intimate connection between brain and culture. This is expressed by the terms enculturation of brain, brain–culture nexus, neuroculture interaction, and encultured brain.

All these concepts aim to describe the intimate relationship between brain and culture. How is it possible for the brain to be deeply entrenched and dependent on its cultural context? Here, I suggest complementing Kitayama and Park's (2010) three-component model with two additional components in order to better understand how the intimate relationship between brain and culture can be generated.

I first suggest to distinguish what Kitayama and Park (2010) subsume under the umbrella term of "psychological and neural tendencies." Specifically, I consider psychological tendencies to be distinct from and to build on the more basic and preceding neural tendencies. Most important, I suggest that both neural and psychological tendencies cannot be considered as mere correlates, with the former being sufficient of the latter. In order for neural tendencies to be transformed into psychological tendencies, processes such as learning as, for instance, probabilistic learning must take place. The mere generation of neural activity that is without any additional learning processes may not be sufficient by itself to allow for transforming culturally sensitive neural tendencies into culturally dependent psychological tendencies. Accordingly, learning and its dependence on the cultural context may account for the culturally sensitive psychological tendencies.

Learning may thus explain why our psychological tendencies are culturally sensitive. However, this leaves open why and how the brain's neural activity is by itself dependent on its respective cultural context and thus culturally sensitive. If learning explains the step from neural tendencies to psychological tendencies, it cannot account for the cultural sensitivity of the neural tendencies themselves. The brain's neural tendencies and their relationship to the world must thus be considered independent of learning and the psychological tendencies. This means that we need to add the brain's neural tendencies as distinct and thus as a fourth key component to the layers of culture suggested by Kitayama and Park (2010).

*Mechanism for Culture–Brain Interaction*

What does this imply for the kind of mechanisms for which we must search? We must seek yet another mechanism besides learning in order to account for the cultural context dependence of the brain's neural activity by itself prior to and independent of any learning processes. Conceptually, this means that we need to add the world as a fifth key component in our model of the different layers of culture. Specifically, we need to explain how the world, and thus our environment and culture, can be transformed into the brain's neural activity in such way that the latter becomes culturally sensitive.

What would such other mechanism that operates prior to and independent of learning look like? Conceptually, we are thrown back to the very basic relationship between brain and world: How and why is the brain always already embedded within the world and thus its various cultures? Philosophically speaking, we are asking for the necessary conditions that first and foremost make possible and unavoidable the dependence of the brain's neural activity on its respective cultural context. In other words, we are searching for those conditions that make the enculturation of the brain necessary and unavoidable.

Neurophilosophically, one may now raise the question regarding the nature of the exact mechanisms. I postulate that the dependence of the brain's neural activity on its respective cultural context, its cultural sensitivity, is related to the way the brain generates and thus encodes its neural activity. Rather than focusing on the neural correlates of both learning and the various psychological functions of the brain, we here search for something much more basic—how the brain generates and encodes its neural activity as such (which then "later" resurfaces in the various psychological functions).

*Enculturation of Brain and Embrainment of Culture*

I here claim to complement the three components in the layer model of culture by a fourth and fifth one. The fourth component is the brain and its neural activity by itself as distinguished from the psychological tendencies, the third component. The fifth component consists of the world or environment—the culture. This raises the question of how the neural tendencies are transformed into psychological tendencies. For this, I assume learning to be central. In addition, it raises the question of how the world and culture are transformed into the brain's neural activity for which the particular strategy that the brain applies to encode and generate its own neural activity may be central.

How is all that related to the questions of the enculturation of brain and embrainment of culture?

The way the world is related to the brain allows for transforming the culture of the former into the neural activity of the latter. One can thus conceptually speak of enculturation of brain. I henceforth postulate that the enculturation of brain is made possible and, most important, necessary and thus unavoidable, by the specific encoding strategy the brain applies to generate its own neural activity. Philosophically or better neurophilosophically speaking, the brain's encoding strategy may then be considered a necessary condition in predisposing and thus making possible the enculturation of brain.

What about the reverse the embrainment of culture? So far, I have considered how culture is transformed into the brain and its neural activity—the enculturation of brain. This left open the opposite direction, namely how the brain and its various functions are transformed into culture—the embrainment of culture. I now build upon the suggested models of different layers that I shall briefly recapitulate in the following.

The first and deepest layer is the world itself, including its various environments and cultures. No matter where or how, any brain on the second layer must link and connect to the first level, the world, in order to generate its own neural activity. This is possible, as I suppose, by applying a particular encoding strategy that shall be specified in the following sections. The generation of neural activity in turn sets the stage for making possible learning with the subsequent transformation of neural into psychological tendencies—the third layer. This is complemented by the fourth layer, the cultural tasks that may find their neural correlates in especially sensorimotor and affective functions. Those, in turn, may make possible the initiation of cognitive functions with the subsequent generation of explicitly held beliefs and values as the fifth and highest level in our layer model of culture.

Does this explain the embrainment of culture? No! All we showed so far is how the enculturation of the brain's neural activity, as based on the interaction between world and brain as the first two layers, is transferred to the three higher layers—psychological tendencies, cultural tasks, and values and beliefs. The higher layers may thus be encultured on the basis of the preceding enculturation of the brain's neural activity. However, this cannot yet explain how the brain and its neural activity are transformed into culture with the subsequent embrainment of culture.

### *Culture–Brain Iterativity*

How can we account for the embrainment of culture? I tentatively postulate that our culture gets embrained by the impact of our brain's sensorimotor, affective, and cognitive functions and their respective cultural manifestations, psychological tendencies, cultural tasks, and beliefs and values. By recruiting our brain's sensorimotor, affective, and cognitive functions, we cannot avoid interacting with the environment and thus the world and its culture. One may want to speak of some kind of feedback of our brain to the culture: Although its own neural activity is based and dependent on its respective cultural context, our brains allow us to actively impact that very same cultural context by instantiating sensorimotor, affective, and cultural functions. Also, because those functions are based by themselves on the cultural sensitivity of the prior encoding of neural activity, any impact of those functions on the culture cannot avoid embraining the latter—embrainment of culture (Figure 2.1).

The philosopher may now want to step forth and argue that such a model is logically circular. Something that is dependent on something else cannot, at the same time, impact that on which it is dependent. In other terms, the something that is, the brain, cannot be dependent on the culture

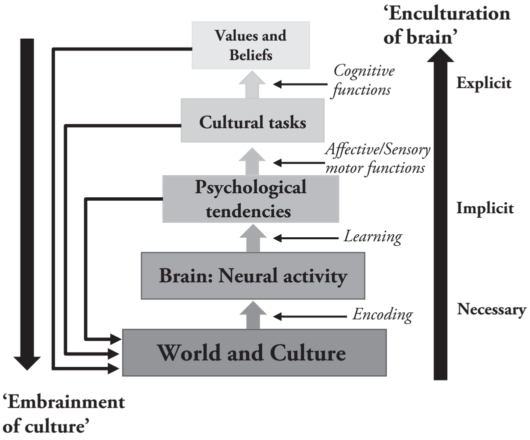

**Figure 2.1** Relationship between culture and brain: Culture–brain iterativity. This figure illustrates the different layers of culture from world to brain, psychological tendencies, cultural tasks, and beliefs and values. Each level or layer is generated on the basis of the former as well as by an additional mechanism as indicated on the right by the small arrows. On the right, the large ascending arrow indicates the enculturation of brain, whereas the large arrow on the left indicates the degree of "embrainment of culture." The latter is achieved by feedback loops of the different levels to the world and its culture.

while at the same time remaining independent of it as when impacting it. Accordingly, taken together, enculturation of brain and embrainment of culture seem to amount to nothing less but logical circularity. That is the logical reality of the philosopher.

What about the empirical reality of the anthropologist and the neurophilosopher? The empirical data show that both enculturation of brain and embrainment of culture seem to go hand in hand; apparently, they are intimately linked with each other. Instead of a circular movement, there seems to be rather an iterative movement between brain and culture: The culture is encoded into the brain's neural activity, which in turn, via its sensorimotor, affective, and cognitive functions, becomes manifested in the culture. That in turn changes the cultural context that provides the very basis for the subsequent encoding of the brain's neural activity.

One may thus want to speak of iterative loops between culture and brain, which I term *culture–brain iterativity.* The concept of culture–brain iterativity describes the reciprocal relationship and mutual dependency between brain and culture. This comes close to other concepts such as "looping" (Vogely & Roepsstorf (2009), based on Ian Hacking), brain–culture nexus (Domingeuz Duque et al., 2010), encultured brain (Choudary, 2010), and neuroculture interaction (Kitayama & Uskul, 2011). The difference between my concept of culture–brain iterativity and these other concepts is that (1) the concept of "iterative" entails a dynamic and reciprocal movement and mutual dependence between brain and culture, and (2) this dynamic that is iterative dependency is necessary and unavoidable, meaning that it would not be possible otherwise (without losing brain and culture as they are in our natural world, as the philosopher would say).

How can we further support such culture–brain iterativity on empirical grounds? Here, I focus on the first and most basic step, the enculturation of brain. This leads me to the question of how the brain generates and encodes its neural activity depending on its respective cultural context. I therefore shift from the previously discussed conceptual questions of culture to the more empirical issues of the brain.

## Empirical Considerations: Generation and Encoding of Neural Activity

We know much about the brain these days. Neuroscience has explored its various molecular, cellular, and biochemical mechanisms. Much progress has also been made with regard to the regional and network levels of neural activity. Functional imaging allows us to investigate how the neural activity of specific regions and networks is related to particular sensory, motor, affective, cognitive, or social functions. This has even brought consciousness and other mental features into the realm of neuroscience, whose neural correlates we search for intensely.

One feature of the brain remains elusive, however. We do not know the brain's neural code—that is, the currency the brain uses to generate and process its neural activity. This may hinder progress and block our insight into the brain's various functions.

We recall from biology. Francis Crick and James Watson's discovery of the DNA as the genetic code has opened new pathways in our understanding of life and has put biology on a new platform. Analogously, unraveling the brain's neural code may enable us to understand why the brain works in the way it does and can generate the various sensory, motor, affective, cognitive, and social functions. In other words, the detection of the brain's neural code may provide a novel, much-needed ground for neuroscience.

### *Encoding of Neural Activity*

What does the term *code* mean? This term is used often to mean a metric or measure that captures and reflects purposeful and biologically or teleologically meaningful activity in a system (DeCharms & Zador, 2000; Friston, 2000). As such, the term code describes a specific processing algorithm or instruction set according to which information is processed in a system. Such processing algorithm as metric or measure remains purely formal by itself; this means that it is yet devoid and prior to the constitution of any contents such as sensory, motor, cognitive, affective, or social contents, as in the case of the brain. The term code is used in the remainder of this chapter in a purely formal way (see also Freeman, 2007, 2011). Taken in this sense, a code allows transforming information from one particular form into another form in order to make possible the subsequent processing of that information.

For instance, the computer codes any kind of incoming stimuli according to 0 and 1, a format that allows the computer to further process the stimuli and their information. Although we do know very well the basic code and its respective format in the case of the computer, we are currently at a loss when it comes to the basic code of the brain, the neural code, and the kind of format it entails. In other words, we currently lack the knowledge of the neural code (e.g., the metric or measure) that the brain applies to the encoding and processing of its own neural activity.

I propose that such basic metric or measure applies to any neural activity in the brain, whether it is stimulus-induced activity or the brain's resting state activity (this distinction is discussed later). The basic metric or measure provides a common code or, more metaphorically stated, a common currency or language for all kinds of neural activities in the brain. This makes possible, for instance, the direct interaction between the different associated functions (sensory, motor, affective, cognitive, social, etc.) and their respective neural networks as it is often observed in functional brain imaging in affective, cognitive, and social neuroscience.

Matters are far from simple, however. Searching for the term "neural code" in the current Internet databases will reveal an abundant and almost inflationary use of this term. The term "code" is used on different levels, ranging from the molecular to the cellular and also population levels to the regional and network levels of the brain's neural activity. Most often, the term *neural code* is intended to describe activity changes at the cellular level as observed in single or multi-unit electrophysiological recordings. This is the case, for instance, in the concept of "rate coding" that describes the carrying (and representing) of information in the neurons' firing rates as the rate of the latter varies with the changes in the former (Friston, 2009; Singer, 1999, 2009).

The term neural code is also often used to describe the temporal constellation of neural activity on especially the population level of neural activity. This is the case, for instance, when one speaks of "temporal coding" or "synchrony coding": Temporal coding describes the neuronal synchronization of different neuron populations and regions across time as observed in recording studies in both primates and humans (Engel & Singer, 2001; Lutz, Lachaux, Martinerie, & Varela, 2002; Rodriguez et al., 1999; Singer, 1999, 2009).

The situation is even more complex, however. Although often associated with the cellular and population levels of neural activity, the term code can also be used on the level of regions and neural networks, the regional and network level. One example is the concept of predictive coding that is often used in the context of functional imaging of different regions during, for instance, reward and mirror neurons (Friston, 1995, 1997, 2000, 2009; Montague, King-Casas, & Cohen, 2006).

The concept of predictive coding proposes that neural activity in particular regions such as the ventral striatum (e.g., during reward) stems from the comparison between predicted and actual inputs. The measure or metric determining neural activity on a regional level thus pertains to a difference: Predictive coding proposes that the neural activity in particular regions is based on the encoding of a difference, the difference between predicted and actual input.

### *Neural Code as "Common Currency" Between Different Levels of Neural Activity*

How do these different forms of neural coding stand in relation to each other? Rate coding, temporal coding, and predictive coding are suggestions for a neural code on specific levels of neural activity—cellular, population, and regional. What remains unclear, however, is how these different levels of neural activity can communicate and interact with each other. To do so, they must share the same code so that, for instance, the single cell's number of spikes translates into population activity and ultimately into the activation of a specific region or even network. Hence, the interaction between different levels of neural activity requires what may be described as "common currency."

Of what does "common currency" consist? Such common currency needs to link the different levels of the brain's neural activity—cellular, population, and regional (and network)—in order to make possible their direct interaction. Only if, metaphorically speaking, the different levels of the brain's neural activity "speak the same language" and "use the same currency" can they interact with each other. What is the "common currency" or "language" of the brain that links and glues its different levels of neural activity together? We currently do not know.

### *Encoding Versus Decoding of Neural Activity*

So far, I have discussed the concept of the neural code as purely formal measure/metric and as "common currency" between the different levels of neural activity. There is yet another feature that needs to be mentioned. The concept of the neural code can be understood in terms of either "encoding" or "decoding" (Friston, 2009; Haynes, 2009, 2011; Kay, Naselaris, Prenger, & Gallant, 2008; Naselaris, Kay, Nishimoto, & Gallant, 2011; Naselaris, Prenger, Kay, Oliver, & Gallant, 2009). The concept of encoding concerns how stimuli and their features are transformed and translated into neural activity. The focus here is on how information from the outside of the brain, such as from the world, generates neural activity: How must the neural activity in the inside of the brain be generated in order to contain some information about the stimuli and their features from the outside world? Accordingly, encoding describes the strategy that the brain applies to generate its own neural activity during the encounter with stimuli from outside of the brain.

This is different in decoding. Unlike in encoding, the focus here is not so much on the generation of neural activity by stimuli from the outside of the brain. Instead, decoding focuses on the information that is contained in the brain's neural activity (Friston, 2009; Haynes, 2009, 2011). The guiding question here is, What information about the outside world and its stimuli and features is contained in the brain's neural activity?

Decoding refers to the information about the outside world as it is contained in the brain's neural activity. This distinguishes it from encoding. Rather than focusing on the information itself as it is contained in neural activity, encoding searches for how the neural activity itself is generated. The brain must generate and thus encode its neural activity in a particular way in order to contain some information about the outside world. Encoding thus precedes decoding in very much the same way as the older twin precedes the younger one.

The difference between encoding and decoding goes along with different methodological strategies in the analysis of brain imaging data such as from fMRI, for instance. This is well expressed in the following quote by Naselaris et al. (2011):

> Most current understanding has been achieved by analysing fMRI data from the mirror perspectives of encoding and decoding. When analysing the data from the encoding perspective, one attempts to understand how activity varies when there is concurrent variation in the world. When analysing data from the decoding perspective, one attempts to determine how much can be learned about the world (which includes sensory stimuli, cognitive state, and movement) by observing activity. (p. 401)

For instance, Kay et al. (2008) observed that the three-dimensional space of the stimuli from natural scenes, the "input space," is mirrored in the space of the stimulus-induced different voxels in visual cortex, the "activity space." Sandwiched between the stimuli' input space and the brain's activity space are the features of the stimuli and their respective space, the "feature space." The feature space provides the translation and thus bridges the gap between the environment's input space and the brain's activity space (Naselaris et al., 2009).

### *Narrow Versus Wide Version of Encoding*

One may distinguish between narrow and wide versions of the concept of encoding. Most generally, encoding describes a formal measure or metric of how neural activity is generated in relation to stimuli and their features. Usually, these stimuli and their features are understood to originate in the environment thus concerning exteroceptive stimuli (Kay et al., 2008; Naselaris et al., 2009, 2011). This is the narrow version of encoding that concerns the encoding of exterocepetive stimuli into neural activity.

In addition to exteroceptive stimuli from the environment, the interoceptive stimuli from the own body also generate neural activity and thus also need to be encoded. Furthermore, as it will become clear later, the intrinsic activity in the brain, its spontaneous or resting state activity, is undergoing continuous changes that also need to be encoded into neural activity. Accordingly, in addition to exteroceptive stimuli from the environment, interoceptive stimuli from the body and the intrinsic activity changes within the brain require some kind of encoding.

This means that the encoding of neural activity cannot be restricted to exteroceptive stimuli alone. Instead, we need to understand the concept of encoding in a wider way that includes all extrinsic stimuli, intero- and exteroceptive, from both body and environment. In addition, we also need to consider the encoding of activity changes that are induced by the brain and its intrinsic activity. Taken together, we need to opt for a wide version of encoding that pertains to any kind of neural activity generated in the brain independent of its origin in environment, body, or brain.

My focus here is on how the brain generates and thus encodes neural activity. Rather than on decoding information from neural activity, my focus is on the encoding and thus generation of neural activity. This pertains to neural activity in general irrespective of its origin in brain, body, or environment. I thus presuppose the wide version of the concept of encoding throughout.

## Neuronal Considerations: Encoding of Neural Activity

So far, we have discussed the concept of encoding and how it must be distinguished from other concepts such as decoding, as well as how it applies to the brain and its neural code. However, this left open (1) the specific encoding strategy that the brain applies to generate and encode its neural activity and (2) how that encoding strategy can account for the here targeted necessary dependence of the brain's neural activity on its respective cultural context—that is, enculturation of brain. This is the focus of the following section.

### *Encoding and Redundancy*

We are bombarded with a multitude of inputs from the environment, such as sensory stimuli including various forms of light intensity and changes in sound pressure, gustatory and olfactory stimuli, and so on. How does the brain process all of these stimuli? Different possibilities exist.

For instance, the brain could process each stimulus by itself, independent of the respective other. In this case, the multitude of stimuli would correspond to the number of active neurons, implying a one-to-one relationship between stimuli and neurons. Such a coding strategy is described as "local coding." Roughly, local coding proposes that each stimulus and, specifically, its physical features such as color and motion are encoded separately in different neurons. Local coding thus proposes a one-to-one relationship between the number of stimuli and the number of active neurons (Figure 2.2).

However, as demonstrated in detail later, such a one-to-one relationship between stimuli and neurons cannot be observed. Instead, the various sensory stimuli are represented by a relatively small number of simultaneously active neurons compared to the large number of neurons present in the brain. Thus, there is a many-to-one relationship between sensory stimuli and active neurons, amounting to what is called "sparseness" in the neuronal representation of sensory input. The sensory inputs are processed and coded in a sparse way—that is, by a number of active neurons lower than the number of stimuli—entailing what is called "sparse coding" (for reviews, see Jacob, Vallentin, & Nieder, 2012; Molotchnikoff & Rouat, 2012; Olshausen & Fields, 2004; Rolls & Treves, 2011; Simoncelli & Olshausen, 2001).

Let us now describe sparse coding in further detail and, in particular, why such sparse encoding of sensory stimuli may be beneficial. When encountering our environment, our brain is confronted with a multitude of stimuli. Not every stimulus is relevant, however.

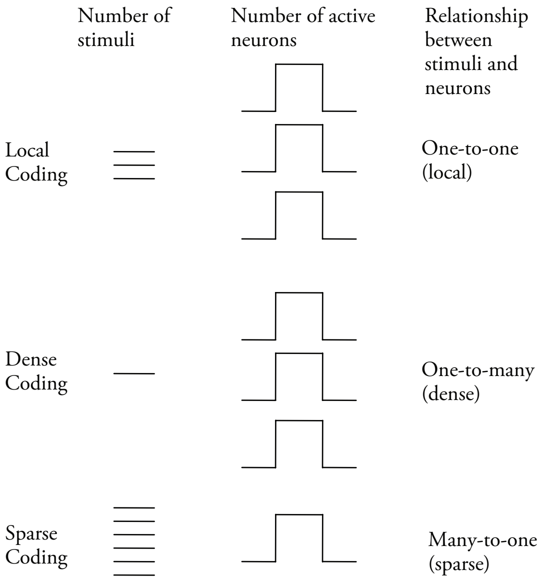

**Figure 2.2** Different strategies of neural coding. This figure shows different possible strategies of encoding stimuli into the neurons' activity. Thereby, the relationship between the number of stimuli and the number of active neurons is central. If their relationship is one-to-one, one speaks of "local coding." If the number of active neurons exceeds the number of stimuli, one speaks of "dense coding." If the reverse is the case—the number of stimuli exceeding the number of active neurons—sparse coding must be assumed.

If, for instance, we hear a bird singing the same tone over and over, it is relevant the first time (if at all) but becomes increasingly irrelevant with each repetition. There are thus plenty of irrelevant stimuli—that is, redundancies. Coding each of these redundant stimuli on a one-to-one basis, as proposed in local coding, would be highly inefficient. One could hear the brain saying (if it could speak by itself as for instance in an imaginary thought experiment), "Why should I waste my precious neural and energetic resources on stimuli that are irrelevant for my owner?"

### *Encoding Strategies*

How do our brains deal with redundancies in sensory input? The British neuroscientist Horace Barlow, born in 1921 as great-grandson to Charles Darwin, focused on this question. Barlow (1972, 2001) suggests that such redundancies in sensory inputs are central and provide important knowledge about our environment that is processed and coded in the activity changes of the brain and specifically in the sensory cortex.

However, this makes it even more difficult for the brain. The brain is confronted with a "difficult choice," as one may want to say in a figurative way: There is plenty of redundancy in the sensory inputs that needs to be reduced, but at the same time such redundancy may contain some useful information. The brain is thus torn between discarding redundant information and retaining information that could be of potential relevance.

How can the brain "deal" with the contradictory requirement of discarding and retaining information at the same time? We already discarded local coding as one possible option because it requires too much effort to encode seemingly redundant information.

Another possible coding strategy could be to select or compress the multitudes of sensory inputs, amounting to what Barlow calls "selective coding" or "compressive coding" (Barlow, 2001, p. 243). Such selective coding retains certain inputs while discarding others. This entails that the latter ones, the discarded inputs, are lost irreversibly; this is problematic, however, because these inputs may potentially be relevant in the future. Hence, selective or compressive coding may be an insufficient coding strategy to deal with the problem of redundancy.

### *"Encoding of the Stimuli" Natural Statistics*

Barlow suggests an alternative strategy to both "local and selective coding." Rather than coding each stimulus by itself, as in local coding, or selecting stimuli, as in selective coding, he suggests that the brain codes and represents chunks of stimuli and their details together, for example, as "gathered details" (Barlow, 2001, p. 248). Let us explain what exactly is meant by "gathered details." These gathered details may, for instance, concern the sensory inputs' frequency of occurrence across the different discrete points in physical time and space. In the previously mentioned example of the singing bird, this raises the question of whether the stimulus occurs with a certain temporal regularity (i.e., the same tone over and over again) and whether the bird's tone occurs in conjunction with other stimuli, such as the moving of leaves (due to the bird's efforts while singing).

How can we specify such encoding strategy? Let us start with what is not encoded into neural activity because that will make it easier for us to better understand the brain's actual encoding strategy. Barlow proposes that the sensory cortex does not encode each tone by itself, including its respective discrete point in physical time and space (e.g., its respective temporal and spatial position). The single tone and its respective spatial and temporal features are not encoded by themselves and thus separate and in isolation from the other tones as proposed in local coding.

After having shown how the brain does not encode, we now can turn our focus to the brain's actual encoding strategy. Instead of encoding single stimuli by themselves, the brain seems to encode the distribution of the stimulus, the tone during the bird's singing, across its different discrete points in physical time and thus the frequency distribution of the tone. The brain may also encode the spatial position of the bird's tone relative to the tree's moving leaves, for instance.

What is encoded into neural activity is thus the statistical frequency distribution of stimuli (e.g., the tone) across different discrete points in physical time and space. This is what Barlow describes as the encoding of the stimuli's "natural statistics," the statistical frequency distribution of a stimulus across different discrete positions in time and space. Rather than encoding each single point in time and space by itself, our brains encode the variability and thus the frequency with which a particular point in time and space occurs. This means that what is encoded into neural activity is rather the variability of that particular point across time and space and thus its statistical frequency distribution. Such encoding of the stimuli's natural statistics is indeed supported by findings especially in the visual and auditory cortex (David, Vinje, & Gallant, 2004; Lewicki, 2002; Olshausen & Field, 1996; Olshausen & O'Connor, 2002; Rozell, Johnson, Baraniuk, & Olshausen, 2008; Simoncelli & Olshausen, 2001; Willmore, Mazer, & Gallant, 2011).

### *"Informational Inefficiency" of Alternative Encoding Strategies*

Encoding of the stimuli's natural statistics implies that several stimuli are encoded by the neural activity of one neuron, entailing a many-to-one relationship and thus sparse coding. Accordingly, sparse coding can tentatively be defined as the neural coding of the stimuli's natural statistics across different discrete points in physical time and space. Before going into empirical detail, I briefly contrast sparse coding with other possible coding strategies with regard to how they stand in relation to the earlier mentioned problem of redundancy.

Instead of only a few neurons being recruited during multiple sensory inputs, a higher number of neurons may respond to most stimuli. For instance, one stimulus may then induce the activity of several neurons. This implies a one-to-many relationship between stimuli and neurons and amounts to what is called "dense coding" (Vinje & Gallant, 2000).

However, such dense coding is highly redundant in that it codes the same sensory input in the activities of many neurons while each neuron contains only a small amount of information. The high redundancy and the small amount of information encoded in the neurons' activity make such dense coding rather inefficient (Vinje & Gallant, 2000). One may thus want to speak of the "informational inefficiency" of "dense coding."

Alternatively, each sensory input may be coded separately by one specific neuron in a one-to-one way, which is described as "local coding" (Vinje & Gallant, 2000). The neurons would then be tuned to give highly selective responses to extremely specific sensory inputs. Given the almost unlimited number of possible sensory inputs, this would require an implausibly large number of neurons.

In addition, each neuron would also need to show extremely specific computational properties as being tuned to only one particular sensory input, if not to only one specific physical feature. However, this is not only empirically implausible but also highly inefficient with regard to the number of required computations and the amount of energy needed for each of the different computations. Informational inefficiency may thus be closely linked to "computational and energetic inefficiency."

### *Informational Efficiency of the Encoding of Natural Statistics*

The inefficiency of both dense and local coding must be distinguished from the apparent efficiency of sparse coding. Sparse coding allows for maximum information to be encoded when generating neural activity on the basis of the natural statistics and thus the spatiotemporal structure across sensory inputs, rather than encoding single sensory inputs. Such sparse coding requires the recruitment of only a few neurons that encode the sensory inputs' statistical structure.

Unlike dense and local coding, sparse coding may therefore be considered a rather efficient way of neural coding by allowing for a good, if not maximally high, ratio between the amount of coded information and the number of neurons that need to be recruited. Because it allows for maximal information transfer and minimal involvement of active neurons, sparse coding is also described as "efficient coding" (Lewicki, 2002; Olshausen & Field, 1996; Olshausen & O'Connor, 2002; Simoncelli & Olshausen, 2001).

Such "informational efficiency" of sparse coding may be closely linked to both computational and energetic efficiency. The number of computations required for the processing of stimuli is lower than the number required in both local and dense coding, so sparse coding may be more computationally efficient. That in turn implies lower energy demands and thus "energetic efficiency." Accordingly, sparse coding and its encoding of natural statistics may be described as an "efficient coding strategy" for informational, computational, and energetic demands (for details, see Northoff, 2013a).

## Neurocultural Considerations: Encoding of "Sociocultural Statistics" Into the Brain's Neural Activity

Can the encoding of the stimuli's natural statistics account for the observed changes in cultural neuroscience? Yes and no. Yes, the data clearly show that the frequency of a particular stimulus or task plays a central role in yielding cultural differences in neural activity. The encoding of the frequency distribution of stimuli and thus natural statistics may therefore be central in generating neural activity.

However, the data go beyond that. They also show that the same stimuli are processed in different ways in different context. This is possible only if the encoding of neural activity is dependent not only on the frequency of the stimuli but also on the frequency of the context in which the stimuli occur. Hence, it is not only the natural statistics of the stimuli themselves that are encoded but also their statistical relationship to their respective social and cultural context. One may here speak of either contextual statistics or, specifically, sociocultural statistics that are encoded into the brain's neural activity.

How can we describe such sociocultural statistics in further detail? What is encoded into the brain's neural activity is neither the single stimulus alone nor its natural statistics. Instead, it is the statistical frequency distribution of the stimulus in relation to its sociocultural context—the stimulus' natural statistics in conjunction with its sociocultural statistics (Figure 2.3).

Let us explicate such encoding dependent on the sociocultural context in further detail. The concept of natural statistics describes that the statistical frequency distribution of a particular stimulus is encoded across time and space. One may thus want to speak of a natural statistical frequency distribution. However, things are not so easy. The very same stimulus may also occur in conjunction

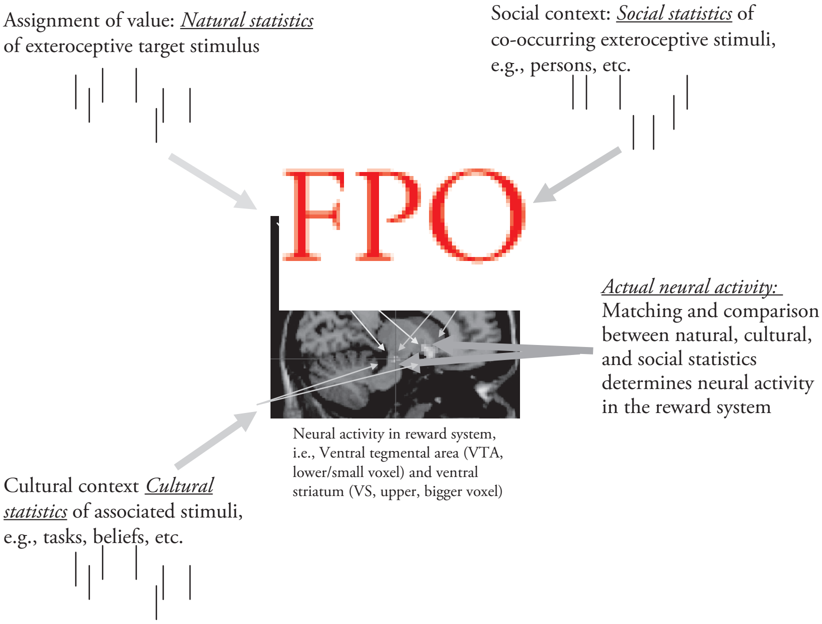

**Figure 2.3** Encoding of neural activity. This figure illustrates that the brain generates its neural activity by encoding different statistical frequency distributions, natural statistics, social statistics, and cultural statistics. We take here the neural activity in the reward system and specifically in the ventral striatum as a paradigmatic example that is supposed to apply to all regions and their generation and encoding of neural activity.

with other stimuli at the same point in time and space in the context of the particular stimulus. That co-occurrence of the particular stimuli with other stimuli may also be encoded into neural activity.

This means that not only the single stimulus and its natural statistics but also its relationship to other stimuli in its respective sociocultural context are encoded into neural activity. The generated neural activity may then be based not only on the natural statistics of our target stimulus but also on its co-occurrence with other stimuli in its respective social and cultural context—its sociocultural statistics. In short, the brain may encode both the natural statistics and the sociocultural statistics of stimuli into its neural activity.

### *Social and Cultural Contexts and the Encoding of Sociocultural Statistics*

Let us give a paradigmatic example of an fMRI study. Using fMRI, Fliessbach et al. (2007) demonstrated that the activity in reward circuitry (e.g., the ventral striatum) was highest when the person in the scanner received $30 in a gambling task and knew that another fictive player got less—that is, $10. However, neural activity in reward circuitry decreased when the fictive player got $60, even though the person in the scanner still received the same amount as before (i.e., $30).

How is this possible? One would expect the neural activity in the reward system to remain the same in both cases because the person receives the same amount of money (i.e., $30). This is not the case, however. Neural activity increased when the person in the scanner received a higher amount than the person outside, whereas the opposite was the case in the reverse scenario. Hence, neural activity in reward circuitry is determined not so much by the actual stimulus and its specifically associated value—that is, $30. Instead, neural activity seems to be determined by the relation between the actual stimulus (i.e., $30) and the stimuli in the respective social context—that is, the other person receiving either $10 or $60.

The study demonstrated that neural activity in the reward system depended on whether the person inside the scanner receives a higher or lower amount of reward than the one outside the scanner. How is that possible? This is possible only when assuming that what is encoded into neural activity of reward is not the absolute amount of the actual stimulus (i.e., $30) the person in the scanner receives by itself. Instead, the relation or the difference between the two stimuli—that is, the difference in the amounts of money between the two persons inside and outside the scanner—must be encoded into the reward system's neural activity.

Both stimuli (i.e., the different amounts of money) are apparently compared and matched with each other, with the result of this process determining the degree of neural activity in the reward system. This means that the social relation signified by the difference between the own and the other person's amounts of money is encoded into the neural activity change of the reward circuitry. Put into our term used previously, this means that what is encoded into the brain's neural activity must be the sociocultural statistics of the reward stimulus—the $30 the participant in the scanner is supposed to receive. Otherwise, by assuming the mere encoding of that stimulus by itself or its natural statistics, we cannot explain the dependence of the reward-related activity on its respective social context.

The same may now apply to the cultural context. The merely statistical co-occurrence of specific stimuli with particular values, beliefs, behavioral patterns, and cultural tasks may be encoded into the brain's neural activity in very much the same way as the social context seems to be encoded. Although this remains to be shown in future experimental designs, one may conceptually then speak of the encoding of sociocultural statistics into the brain's neural activity.

The concept of sociocultural statistics means that in addition to the natural statistics of the target stimulus, its statistical occurrence with other stimuli in its respective social and cultural context is also encoded into the brain's neural activity. Such encoding of sociocultural statistics may then be the empirical mechanism that may eventually underlie what was described previously conceptually as enculturation of brain—the transformation of world and culture into the neural activity of the brain. Accordingly, if correct, the brain's encoding strategy may have not only major empirical but also conceptual ramifications that shall be indicated briefly in the next section and the remainder of the chapter.

### *Encoding and Cultural Neuroscience*

Cultural neuroscience and its results seem to lend some indirect support to the encoding of the related sociocultural statistics into neural activity during perception. However, this is only indirectly inferred from the current data and needs to be demonstrated more directly in future experimental investigations. In contrast to perception, there are no data on the encoding of natural statistics let alone socionatural statistics in the case of mental features such as the self. Here again, the data from cultural neuroscience on the self suggest that the encoding of neural activity during mental features such as the self seems to underlie the same kind of encoding strategy as during purely physical features in perception.

Future investigations should therefore examine whether the activity during self-specific stimuli is based on the encoding of their natural and sociocultural statistics. Cultural neuroscience provides the rational and background evidence for such an hypothesis that, if true, will have far-reaching implications for our understand of mental features in general (Northoff, 2013a, 2013b).

In summary, it can be seen that cultural neuroscience can clearly benefit from consideration of the brain's encoding strategies, the encoding of the stimuli's natural statistics. At the same time, cultural neuroscience can enrich the debate by showing that the assumption of the encoding of natural statistics needs to be complemented by considering the stimuli's sociocultural statistics as the mechanism underlying the enculturation of brain. This in turn will lead to exciting new experimental approaches that reverberate far beyond cultural neuroscience into neuroscience in general and its investigation of how the brain's neural activity brings forth mental features such as self, consciousness, and others that as such are universal though particular in their respective contents that are culturally dependent.

## Neuroconceptual Considerations: Cultural Neuroscience, Neurophilosophy, and Psychiatry

### *Enculturation of Brain as the Statistically Based Virtual Extension of the Brain's Neural Activity Into the Environment*

What does the enrichment of the natural statistics by the encoding of the sociocultural statistics imply for our characterization of the brain and its neural activity? The concept of the brain and what it is and how it functions in principle is a central concern of neurophilosophy. What is the brain? And how does it function?

The brain's neural activity is often taken for granted and taken as fact in neuroscience in general and cultural neuroscience in particular. The neural activity is simply presupposed and taken as a given. What is then investigated is how stimuli and tasks induce neural activity and how that is distributed in different regions and networks. In contrast, the generation of neural activity by itself prior to and independent of any particular stimuli or tasks and a specific region or network is rarely considered by itself. This was the focus of this chapter.

We demonstrated that the brain may generate its neural activity by encoding the stimuli's natural statistics rather than the single stimulus itself into neural activity. This, as I suggest here, needs to be complemented by the encoding of the stimuli's sociocultural statistics.

What does this imply for the characterization of the brain? The brain's neural activity may then no longer be localized in and reduced to the inside of the brain and its anatomical structures. Although it is manifest there, the brain's neural activity extends beyond the physical boundaries of the brain in a statistically based way to the sociocultural context, the environment. Also, it is this statistically based virtual extension of the brain's neural activity that may make possible the apparent constitutive context dependence of its neural activity, including its necessary (i.e., unavoidable) dependence on the cultural context—the enculturation of brain.

### *Brain-Based Versus Brain-Reductive Approaches in Cultural Neuroscience and Neurophilosophy*

The statistically based virtual extension of the brain's neural activity beyond its own physical boundaries and anatomical structures has important implications for both neurophilosophy and cultural neuroscience. If the brain does indeed encode its neural activity depending on the natural and sociocultural statistics, it may shed a novel light on how the brain's purely neuronal states are able to generate mental features such as self and consciousness.

The mental features and their underlying neural activity can then no longer be reduced to and localized within the brain. Instead, mental features may then be associated with the statistically based virtual extension of the brain's neural activity into its sociocultural context. This not only provides new ideas and hypotheses for future experimental testing in neuroscience (Northoff, 2013b) but also has conceptual implications for neurophilosophy.

Neurophilosophy can then no longer argue that mental features can be reduced to the brain, thus pursuing a brain-reductive approach. Instead, mental features are brain-based rather than brain-reductive, which more generally implies a brain-based rather than brain-reductive form of neurophilosophy (Northoff, 2004, 2014). Cultural neuroscience may be one of the prime witnesses and supporters of such a shift from a brain-reductive to a brain-based neurophilosophy. Why? Because nowhere else can it be better seen than in cultural neuroscience that the brain and its neural activity are apparently intrinsically and thus constitutionally dependent on its respective sociocultural context.

This also reverberates into cultural neuroscience. As stated initially, there is much discussion in cultural neuroscience to explain the cultural context dependence. Our neurophilosophical excursion sheds a novel light on this debate: It shows that it is the brain itself and how it encodes its neural activity that makes it necessary or unavoidable that any neural activity is dependent on its respective sociocultural context by default.

Like neurophilosophy as its theoretical sibling, cultural neuroscience may therefore be characterized as brain-based rather than brain-reductive. Cultural neuroscience may pave the way here for its older empirical sibling, neuroscience in general, which then may be able to possibly reach an understanding of why the brain yields mental features on the basis of its particular strategy of encoding its own neural activity.

### *Cultural Dependence of Symptoms in Psychiatric Disorders Such as Depression*

One may now want to argue that such a brain-based approach is merely conceptually relevant. This is not the case, however. We previously demonstrated that a brain-based approach is essential in understanding the brain's encoding strategy—its encoding of the stimuli's natural and sociocultural statistics. Presupposing a merely brain-reductive approach, one would probably stop at the encoding of the stimuli's natural statistics while neglecting the additional encoding of their sociocultural statistics.

How is such encoding of the stimuli's sociocultural statistics manifested in our behavior? It was previously mentioned that many results, if not most, from cultural neuroscience lend empirical support to such an encoding strategy. Another example is psychiatric disorders such as depression. Here, developmental and thus sociocultural and neuronal aspects are strongly intertwined, which, as I tentatively assume at this point in time, may be possible only on the basis of the brain's encoding of the stimuli's sociocultural statistics. Are depression and its symptoms dependent on its respective context? If so, one would expect, for instance, cultural differences in depressive symptoms. Are their cultural differences in major depressive disorder (MDD)? MDD has been observed to occur across all geographical areas studied, although with transcultural differences in symptom presentation and prevalence estimates (Ballenger et al., 2001). Somatic symptoms, due to heightened interoceptive awareness (IA) in MDD, have often been regarded to occur more often in non-Westerners (Arnault, Sakamoto, & Moriwaki, 2006; Ryder, Bagby, & Schuller, 2002; Ryder et al., 2008), although questions as to this position are raised by the fact that somatization is also often observed in Western cultures (Kirmayer, 2001; Kirmayer & Groleau, 2001). What is clear, however, is that the cognition and determination of the self as mediated culturally strongly impact on the symptoms and course of depression (e.g., see Kirmayer, 2001), thus requiring research that focuses on cultural neuroscience and psychopathology (Choudhury & Kirmayer, 2009).

What remains unclear is whether these transcultural differences are related to depression itself, thus being a feature of MDD, or whether they are related to a more basic transcultural difference that is already present in healthy subjects. This is even more important to consider given the fact that psychological studies (Markus & Kitayama, 1991, 2003) demonstrate differences in IA and exteroceptive awareness and self-referential processing between Eastern and Western cultures (Ma-Kellams, Blascovich, & McCall, 2012).

These points raise the question as to whether the transcultural differences in depression are a feature of MDD or whether they reflect a principal East–West difference in the definition of one's self being present already in healthy subjects. The study of depressive symptomatology has shown that Chinese patients endorsed a higher proportion of somatic symptoms and that Chinese participants also used more somatic words when describing emotional experience compared to Westerners (Yen, Robins, & Lin, 2000). A growing body of research supports that somatization reflects a poor interoceptive awareness—that is, such somatization suggests a culturally bound tendency to misperceive one's own internal states (Aronson, Barrett, & Quigley, 2001;Bogaerts et al., 2008; Gardner, Morrell, & Ostrowski, 1990). However, to date, little research has examined potential underlying neuronal mechanisms due to transcultural differences.

It is clear, however, that the observed cultural sensitivity of depressive symptoms may be closely related to the encoding of sociocultural statistics. Only if the social and cultural context is transformed and specifically encoded into the brain's neural activity can the latter generate symptoms in pathological states such as depression that by themselves are culturally sensitive. Although largely speculative, one may therefore suggest that the encoding of sociocultural statistics may open new doors not only to cultural neuroscience in particular and neuroscience in general but also to psychiatry.

## Conclusion: Fruitful Marriage Between Neurophilosophy and Cultural Neuroscience

This chapter demonstrated that mutual and bilateral exchange between cultural neuroscience and neurophilosophy may be helpful for both disciplines. Neurophilosophy (and also neuroscience in general) may gain a deeper and broader understanding of the brain by considering the cultural context dependence—that is, enculturation of brain—as investigated in cultural neuroscience. This may contribute to a better understanding of how the brain generates mental features as it is relevant for neuroscience in general as well as to the development of a more complex brain-based rather than brain-reductive form of neurophilosophy. Such a brain-based approach may then help us to explain the bilateral and iterative relationship between brain and culture—the culture–brain iterativity—as it is manifest in both enculturation of brain and embrainment of culture.

Conversely, cultural neuroscience may benefit from a side view on neurophilosophy. This provides different strategies of how the brain generates and encodes its own neural activity, which may then be tested for their empirical plausibility in cultural neuroscience. This may result in novel experimental approaches in cultural neuroscience that focus more on the encoding and the sociocultural statistics of the culturally varying contents than on the contents themselves and their respective sensorimotor, affective, and cognitive functions. This will make it possible for us to understand why and how the brain and its neural activity are necessarily dependent on the cultural context—that is, why and how there is enculturation of brain rather than cultural independence with what may be described as "isolation of brain." Finally, by considering the encoding of the sociocultural statistics in the brain's neural activity, cultural neuroscience may serve as paradigmatic and exemplary model for our understanding of the brain in general and thus other domains and branches of neuroscience including psychiatry.

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CHAPTER

# 3

# Sensory Enculturation and Neuroanthropology: The Case of Human Echolocation

Greg Downey

## Abstract

Neuroanthropology seeks to bring the broadest possible account of cultural variation into our understanding of the human brain's potential, expanding the methods we use to trace the envelope of human neurodiversity and the trajectories of neurological development to include robust qualitative and ethnographic methods in natural settings. My research has focused on athletes and other highly trained individuals who demonstrate both the range of activity-induced neuroplasticity and the characteristics of regimes under which this plasticity can be deployed in systematic ways. They also demonstrate how cultural expectations, daily activities, and aversions to activity can inculcate or exacerbate disability. Neuroimaging data may not always be available, especially given the whole-body nature of these activities in ecologically valid settings and the circumstances of anthropological field study. Nevertheless, neuroanthropology argues that neurologically plausible accounts of the abilities that our subjects demonstrate and the experiences that they report are both possible and theoretically productive.

**Key Words:** neuroanthropology, neurodiversity, ethnography, development, neuroplasticity

Neuroanthropology seeks to bring the broadest possible account of cultural variation into our understanding of the human brain's potential, expanding the methods we use to trace the envelope of human neurodiversity and the trajectories of neurological development to include robust qualitative and ethnographic methods in natural settings (Lende & Downey, 2012). My own research has focused on athletes and other highly trained individuals. These individuals demonstrate vividly both the range of activity-induced neuroplasticity and the characteristics of regimes under which this plasticity can be deployed in systematic ways, but they also demonstrate how cultural expectations, daily activities, and aversions to activity can inculcate or exacerbate disability (Downey, 2010). Neuroimaging data may not always be available, especially given the vigorous, whole-body nature of these activities in ecologically valid settings and the challenging circumstances of anthropological field study. Nevertheless, neuroanthropology argues that neurologically plausible accounts of the abilities that our subjects demonstrate and the experiences that they report, such as sensory alteration as a result of systematic training, are both possible and theoretically productive (e.g., Downey, 2007, 2012a, 2012b).

This chapter takes the example of training in and experiences of human echolocation, especially among the blind. The case of echolocation shows how the careful documentation of extant neurodiversity can help us to better understand simultaneously what the brain is capable of but also how patterns of variation that we might call "culture" are inculcated, including in sense perception. Echolocation in the blind suggests that the study of highly skilled populations may be a crucial route to explore human brain–culture relations or patterns of "neurodiversity," beyond what Andreas Roepstorff (2013) describes as "mapping out gross differences between abstract categories of millions, or indeed billions of people, like North Americans, East Asians, Chinese, or Danes" (p. 61). Cultural neuroscience needs a more anthropological appetite for cultural variation, even if this makes sampling more difficult and requires exploring where we have no preexisting, overarching explanatory mechanisms, such as a contrast in types of selves, with which to easily make sense of what we find.

To use cultural neuroscience to decrease the disparities in population health indicators, we must understand more broadly the ways that developmental contexts shape neurological conditions. The example of Daniel Kish and World Access for the Blind encourages us, as Vogel and Awh (2008) advocate, to think more strategically about how we use interindividual variation to understand human neurological potential and brain functioning (see also Kanai & Rees, 2011). Cultural variation, including a wide range of occupational and other skills, may provide naturally occurring experiments (Cronbach, 1957)—manipulations of the nervous system over developmental time more ambitious than anything possible in a laboratory setting. These alternative ways of developing the human nervous system may reveal to us healthy states and compensatory opportunities impossible to perceive in neurotypical populations, especially in a narrowly confined population of WEIRD subjects (Western, educated, industrialized, rich, and democratic; Chiao & Cheon, 2010; Henrich, Heine, & Norenzayan, 2010). One need only consider shifts in the prognosis for neurological recovery following stroke in recent decades, including the changes wrought by researchers such as Edward Taub, to recognize how our understandings of the human nervous system shape the actual abilities that people develop (Murphy & Corbett, 2010; Taub, 1994).

## Developing Echolocation

In 2012, I shadowed mobility specialist Daniel Kish when he worked with a number of blind children in Canberra. As a mobility specialist, Kish helps the blind to adapt, instructing them in a wide range of techniques, such as how to develop routes for daily activities, observe the environment to extract more information about one's surroundings, and use technologies such as a cane to better navigate. Unlike the vast majority of mobility specialists, Kish is himself completely blind. By the age of 13 months, he underwent complete enucleation of both eyes to combat retinoblastoma, an aggressive form of cancer that strikes the immature retinal cells. Enucleation involves removing entirely the eyes, leaving behind the lids, muscles, and other structures of the empty sockets. Defying many specialists' criticisms (that a blind individual would not be able to teach others mobility skills), Kish became the first blind person certified as a mobility specialist in the United States. He also went on to complete multiple master's degrees and become president and founder of World Access for the Blind, a US not-for-profit that "facilitates the self-directed achievement of people with all forms of blindness, and increases public awareness about the strengths and capabilities of blind people" (World Access for the Blind, http://www.worldaccessfortheblind.org).

Kish's training sessions in Canberra were unusual for a mobility specialist, not simply because the instructor was blind but also because he teaches, among other techniques, a form of active echolocation he calls "flash sonar." Kish uses tongue clicks to generate echoes with which he can perceive space, detect objects, lead hikes, and even ride a mountain bike. Internationally renowned for his ability—Kish has appeared both at the TED conference and alongside Bollywood heavyweight Vikram in a feature-length movie—Kish, like the other instructors working with World Access for the Blind, travels relentlessly to teach echolocation as part of a comprehensive strategy for improving blind people's mobility, independence, and freedom. Beginning with research for his master's degree in psychology (Kish, 1995), Kish has steadily refined his teaching techniques over almost two decades of intensive training and interaction.

In the central courtyard of the National Museum of Australia, an irregularly shaped space with a wide range of obstacles and objects to perceive, Kish encouraged his students to refine their skills at echolocation, whatever their level of expertise. Although I was struck by many things that day shadowing Kish, one of the most fascinating was that he assumed that the children were already echolocating, even if they were meeting for the first time and even if their parents did not know their children could sense space through sound. Kish did not so much demonstrate echolocation to the blind children as encourage them to rely more upon a sense they already had while he sought to articulate explicitly what they could perceive through sound. He gave them tasks that pushed their ability to perceive space through sound and provided feedback on their technique, pointing out, for example, when a child was clicking too rapidly to assimilate the information or not scanning the space sufficiently to build up a broad image of the surroundings.

Kish assumed that his young students could perceive through a sensory channel that was invisible to the vast majority of sighted individuals, even if we unconsciously make use of information gained by echolocation (Stroffregen & Pittenger, 1995, p. 183). The clicks he made were so innocuous, so subtle, that, sometime later during a seminar, I had to challenge him, "You can't *really* hear echoes from a click that's so soft?!" Before he could respond, another blind person in the seminar retorted, with some amusement, "You mean you *can't*?" Carefully controlled testing has shown that Kish and other expert echolocators with World Access for the Blind, in fact, do *not* have exceptional hearing when it comes to measures of basic sensory acuity and thresholds (e.g., Thaler, Arnott, & Goodale, 2011). However, on more complex tasks of perceptual skill in hearing, many of them demonstrate extraordinary ability.

The case of human echolocation demonstrates the degree to which human senses are trainable, especially given appropriate feedback and social support. Although Daniel Kish's sensitivity may be unusual, and the extraordinary degree of neural plasticity demonstrated in echolocation may require sensory deprivation, the pattern of refinement is a hallmark of how sensory systems actively develop and are susceptible to variation. Evidence both from studies of perceptual learning and from the anthropology of the senses points to sensory variation as an important area of cultural variation (for reviews, see Herzfeld, 2001; Howes, 1991, 2003). Yet sensory variation has thus far been little explored by cultural neuroscientists (with some noteworthy exceptions, such as Chua, Boland, & Nisbett, 2005; Gutchess, Welsh, Boduroglu, & Park, 2006; McClure et al., 2004). The fact that all blind people are not expert echolocators suggests that deprivation of sense input, or the availability of useful sensory information, alone is not sufficient to produce sensory prowess: Culture includes an "education of attention," to borrow from J. J. Gibson (1966, 1979), which has import neuropsychological consequences. In particular, the explicit discussion of echolocation by Kish and World Access for the Blind opens up the possibility of a beneficial skill-refining "looping effect," as Ian Hacking (1995) describes: An underdeveloped and largely inchoate sensory channel can be made socially explicit, even subject to scientific investigation, and subsequently liable to structured training. Kish, for example, points to a university lecture in psychology on human echolocation as a watershed moment in his own understanding of his sensory abilities, leading to his master's thesis and eventual career in training the perceptions of the blind.

## Human Echolocation in Neuroanthropological Perspective

Dating back to the eighteenth century, commentators noted that blind people had the ability to perceive space and physical objects (Diderot, 1749), but until the 1940s, this ability was poorly understood. Psychologists and the blind alike referred to "face vision" or a kind of "obstacle sense," a tactile sensation like pressure on the face when approaching a wall or other large object. Not until early experiments led by Karl Dallenbach at Cornell University was it clear that the perception was actually auditory (Cotzin & Dallenbach, 1950; Supa, Cotzin, & Dallenbach, 1944; Worchel & Dallenbach, 1947). Dallenbach's team found that sound-dampening interventions, such as making participants wear socks on carpet rather than hard-soled shoes on wood floors, interfered with blind subjects' ability to detect obstacles. Although some research took place subsequently, by the late 1990s, Arias and Ramos (1997) argued that psychoacoustical research on human echolocation still remained scarce and unsystematic.

Since then, a number of researchers have explored the ability of humans, including novices with normal sight, to navigate by echolocation (see especially Schenkman & Nilsson, 2010; Stoffregen & Pittenger, 1995; Teng & Whitney, 2011; Thaler et al., 2011). Although some of these experiments prevented the blind from actively producing sound, in fact, blind individuals use a wide range of techniques for producing sound; another informant discussed how high heels, for example, could generate sharp clicks and clear echoes in a workplace setting where she wished to keep her echolocating discrete. Kish advocates the use of a sharp, short (10-ms) palatal click, produced by a rapid move of the tongue backwards and downwards from the roof of the mouth behind the teeth, which he argues is the most effective tone for echolocating (see also Rojas, Hermosilla, Montero, & Espi, 2009). Although some advocates for the deaf have proposed using artificial sound generators, the fine control and perception of the original sound from self-generated clicks better allows echolocators to interpret precisely the significance of echoes (Jones, 2005).

Echolocation relies on the fact that sound travels approximately 300 m/s. A sound produced close to the ears will travel out before reflecting back off a solid surface or other object, producing a slight time delay called the "pulse-to-echo" gap. In addition, the relative loudness of the echo in each ear can help the echolocator to fix a direction to the origin of the echo; expert echolocators have been found to be sensitive to variations in angle to an object of as little as 3° of horizontal displacement (Thaler et al., 2011). Other qualities of the sound, including the pitch of the echo, can reveal additional information about the size, surface quality, and even the shape of the object, although all of the psychoacoustic mechanisms involved are not fully understood (Teng & Whitney, 2011). For example, Schenkman and Nilsson (2010) found that some of their blind subjects had exceptional echolocating ability, reliably perceiving a 50-cm aluminum disk at a distance of 4 m. Kish has demonstrated the ability to trace the outline of cars, detect the foliage on trees, and even sense tree trunks through passive echolocation, perceiving auditory shadows in the sound of a creek on one side of a path and auditory reflections from trunks on the opposite side when we walked together in a rain forest reserve. Teng, Puri, and Whitney (2012) suggest that the acuity of echolocation in experts can reach similar levels as peripheral vision in the sighted.

The time lag between the original sound and the echo, however, can be so brief that subjectively, no pulse-to-echo gap exists, as the two sounds perceptually blend into one. From reports of consciously observed sound sensitivity, humans should not be able to perceive objects at short distances (less than 2 m) because the sound and echo become indistinguishable (Stoffregen & Pittenger, 1995, p. 189). However, early research by Kellogg (1962) found that blind subjects were able to detect the distance to an obstacle between 30 and 120 cm away to an accuracy within 10 cm. The pulse-to-echo gap resulting from that distance is actually quicker than the action potential of neurons, the delay caused by an additional 10 cm of sound travel below the theoretical floor of temporal perception, prompting neuroethologist Camhi to observe that "the neural mechanisms responsible" for the acuity "are entirely obscure" (1984, p. 180; cited in Stoffregen & Pittenger, 1995, p. 189).

The pulse-to-echo gap, then, is not the only acoustic property that can give some impression of space; volume, pitch, alteration, interference, and timbre of the echo can all be affected by reflection. Kellogg (1962) found that his subjects could discern such subtle qualities as the difference between denim, wood, or metal. Even sighted people can be surprisingly acute perceiving through sound. For example, we sometimes judge how far away a familiar sound is by how loud it is, remaining calm despite traffic noise because the din is sufficiently quiet to signal our distance from an intersection. In our conversations, Daniel Kish discussed research and his own observations that, at close range, the phase interference between outbound and inbound sonic waves might actually be the foundation for perception; the pitch of a sound appears to change because outbound and inbound sound waves, although they are too close to tell apart, interfere with each other. (For a much more in-depth discussion of the information potentially available in reflected sound, see Stoffregen & Pittenger, 1995.)

Functional magnetic resonance imaging (fMRI) carried out by Thaler et al. (2011, pp. 3–4) found significant blood oxygen level-dependent activity (BOLD) in the primary visual processing area, the calcarine cortex (V1) in experienced echolators, including Kish, when listening to recordings with echoes. Recordings with the echoes artificially stripped out did not cause the same level of activity in these cortical areas, responsible for initial visual processing in normally sighted individuals. The use of "visual" cortical areas in echolocation may be a result of cross-modal plasticity in the absence of visual stimulation (Bavelier & Neville, 2002; see also Sadato et al., 1996) or might arise from the fact that the "visual" cortex is actually specialized in handling spatial information, whichever sensory mode delivers that information (Pascual-Leone & Hamilton, 2001). Thaler and colleagues (2011, p. 10) conclude that, no matter the mechanism underwriting the neurological redeployment, "from a more applied point of view, our data clearly show that EB and LB use echolocation in a way that seems uncannily similar to vision."

One irony of this extraordinary ability, then, is that it likely involves redeploying familiar neurological resources, so much so that Kish has even found that some naive echolocators, who are experiencing gradual degradation of their vision, may not even realize the degree of their own blindness. The sensations offered up by echolocating may convince them that they can still see as they unconsciously compensate by switching sensory modality for perceiving objects at a distance. Although the neural substrates of human echolocation and its potential acuity are both fascinating, to understand the cultural dimension of sensory development, the cross-modal sensory misrecognition is telling, as is the fact that many blind people never refine echolocation abilities, and some even fail to recognize that they are echolocating. After all, if a sensory channel was overdetermined by genetic endowment, fixed neuroanatomy, or simply perceptual opportunity in the environment, all blind individuals would be expert echolocators and misrecognition of echolocation would be impossible. The variability of the ability points to the complex process through which it can emerge.

## The Anthropological Importance of Not Sensing

As philosophers Schwitzgebel and Gordon (2000) note, normal sighted humans *do* echolocate, although not consciously and with much less acuity than virtuosos such as Kish. Teng and Whitney (2011) found that, according to some measures, some, but not all, sighted subjects could be trained quickly to acuity levels approaching those of expert blind individuals. The relative ease of acquiring echolocation highlights a crucial fact (even if inter-individual variation exists in this ease; see Hambrick et al., 2014): Most of us, most of the time, operate well below the theoretical maximum of human sensory acuity. The same echoes that Kish can use to discern his environment most sighted individuals fail to perceive, even though they are well above even an untrained sensory threshold (see also Wallmeier, Geßele, & Wiegrebe, 2013).

The cultural influence on normally sighted individual neglects or actively suppresses awareness of the ability to echolocate, providing no practical scaffolding or social alert to the possibility of perceiving in this way. When Kish talks to students, assuming that they already have the ability to echolocate, and encourages them to elaborate and rely on these perceptions, he is providing social support and sensory reinforcement that is necessary in the vast majority of cases for blind individuals to become expert echolocators. In other words, visual deprivation and neurological opportunity alone are not sufficient to produce the ability to echolocate.

It is true that the blind tend to be more sensitive to the information in echoes, even if they are not conscious of this fact (Dufour, Després, & Candas, 2005; Merabet & Pascual-Leone, 2010). However, when psychologists Schenkman and Nilsson (2010) studied echolocation in blind subjects, they found only 2 out of 10 had well-developed abilities:[1]

> Some blind people may have developed remarkable abilities for the detection of repetition pitch as well as loudness discrimination, which may be the case for the two high-performing blind persons. They are both successful in their respective professions, and our impression is that they are active and mobile. They do not use a guide dog, and appear to be very attentive to acoustic information in the environment, including proficiency in object detection. (p. 496)

Although drawing any conclusions from this sort of off-handed discussion is clearly impossible, the discussion of both guide dogs and attention to acoustic information is telling. Working with a dog is itself a skill and likely would compete for attention with one's own awareness of the acoustic environment. Attention does not merely draw in some dimensions of the sensorium; it actively excludes dimensions of information, such as echoes in ambient sound. Moreover, Kish is explicit that only depending on echolocation for day-to-day activities can produce sensory refinement. World Access for the Blind sponsors a mountain biking team, Team Bat, not simply as a publicity stunt but because echolocation requires sensory challenge and social motivation (see also Thaler, 2013).

The low rate of "high-performing" echolocators, especially those who consciously and actively use sound to map space, confirms a key principle in Kish's teaching: Blind children need to be strongly encouraged to actively click and listen. Stoffregen and Pittenger (1995) note that active echolocation—what Kish calls "flash sonar"—is distinctive as a form of sense perception because it is a "closed-loop system"; that is, "stimulus energy that is generated by the animal propagates into the environment, is structured by the environment, and returns to receptors" (p. 209). Stated simply, to echolocate, people (like most echolocating animals) must *produce* as well as *perceive* sound; most sensory experiences (except arguably taste and touch) are passive, not requiring much effort to create sensation (but see Gibson, 1966).

The active nature of echolocation as a sense means that the perceiver can query the environment, pushing out sonic energy, clicking more frequently or loudly, to generate greater amounts

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[1] Thaler (2013, p. 1) suggests that "perhaps between 20% and 30% of totally blind people" may use echolocation.

of reflected incoming perceptual data, but it also means that passive receptivity is likely not sufficient for the sense to become fully developed. If a blind individual (or non-blind individual, for that matter) does not actively produce sound, testing and acting on the information in echoes, the sense will not develop. Kish works hard to get his students to actively probe the environment with sound rather than just take advantage of ambient noise or engage in passive echolocation.

Kish argues that one of the reasons why he needs to engage in social activism is because sighted individuals, including parents, may unwittingly discourage blind children from emitting these kinds of sounds or engaging in the sort of exploratory practices, such as head movements, clapping, or tapping their feet, that assist the development of echolocation and passive sound location. According to Kish, some parents and other observers think of these actions as "blind-isms," stereotypical movements or activities that blind people do because they cannot see. Sighted individuals can inadvertently short-circuit the acquisition of echolocation if they discourage blind individuals from engaging in these actions because they are not "normal" and draw attention of sighted observers to the individuals' blindness (Molloy & Rowe, 2011). A cultural interpretation of these activities, including social stigma, can negate strategies of exploration and active engagement with the world. Without sufficient social reinforcement, and against stigma in the sighted world, the early developmental stages of an emerging ability to echolocate can become arrested in an underdeveloped state.

Daniel Kish even cited a short paper by Dr. Steven Charles, a specialist in retinal reattachment in premature children (Charles, 2004). Charles insisted that he observed "chirping" and distinctive head-searching movements in blind infants, even when still in the hospital nursery. The implication is that they were seeking to initiate sonic relations with the environment, a fact Charles only recognized because of his work with World Access for the Blind. Because of the infants' own inability to move, and because no one in the nursery would have even thought to engage with this active sensory searching (unless they were themselves blind, perhaps), the infants' initial explorations would fail to get any feedback or sufficient support. Active echolocation would more than likely atrophy. Whereas vision was, in some ways, phenomenologically self-confirming, echolocation for an immobile infant was not, so there was no looping reinforcement of perception and confirmation, either individually or socially.

The necessity of active, exploratory sound-making for echolocation to develop also highlights a key absence in contemporary cultural neuroscience models raised by Andreas Roepstorff (2013, p. 62). Roepstorff points out that even the "gene–culture–coevolution model" fails to include recognition of the active role that individuals play in their own neurocultural development. To develop echolocation, it is not enough to be at the intersection of gene and culture; one must actively query the environment, calling out to create the sensory input that will steadily refine the sensory system itself. In the case of Kish, his active role is crucial, not just in the development of his own abilities but also in the socially contagious way that his activities are influencing how other blind people act, perceive, develop, and, ultimately, function neurologically.

## Culture and the Senses

Research on sensory variation and perceptual acuity across cultures is a long-standing area of collaboration between anthropology and neuropsychology, dating back to some of the founding figures of our disciplines. Franz Boas, widely credited with being the "father" of North American anthropology, began his academic career at the University of Kiel with a dissertation on the problem of the color of seawater; 6 of his first 10 publications were on Fechnerian psychophysics (Stocking, 1992, p. 311). Boas initially worked with Wilhelm Wundt in Leipzig in psychology, but in 1883, he traveled to Baffinland in Canada for a yearlong sojourn among the Inuit, where he sought to extend his research in psychophysics. Once he returned from his fieldwork in the Arctic, he became increasingly convinced that psychophysics alone could not explain perception because of the influence of "situational" or cultural factors (see Harkness, 1992; Stocking, 1965, p. 142ff.).

Similarly, in 1898, the Torres Straits Expedition of Cambridge University, one of the foundational fieldwork projects of British anthropology, was primarily envisioned as a collaborative investigation of the "acuity for each of the basic senses" in a "primitive" society (Haddon, 1901). W. H. R. Rivers tested visual perception; C. S. Myers ran experiments on hearing, smell, and taste; and William McDougall examined the Torres Straits Islanders' haptic senses, including pain tolerance. The research was in part motivated by observations of colonial officials, missionaries, and travelers that the Papuans, like other non-Western peoples, seemed to have superior sensory powers. This view supported Herbert Spencer's theories of the evolutionary transition from "primitive" to "civilized" states involving a shift away from sensory dominance or the "simpler faculties" in experience toward greater reliance on "reason" (Rivers, 1901).

When Rivers recovered from his initial seasickness, severe sunburn, and shock at nearly being shipwrecked, his first research task was to test the color vision of the Torres Strait Islanders. He found that their language possessed no word for the color "blue"; they freely called the sky the same color term as darkness. However, the Torres Strait Islanders possessed no special sensory power. As Henry Head (1922) wrote in his obituary, Rivers

> was able to explode to old fallacy that the "noble savage" was endowed with powers of vision far exceeding that of civilised natives. Errors of refraction are, it is true, less common, especially myopia. But, altogether the feats of the Torres Straits Islanders equalled those reported by travellers from other parts of the world, they were due to the power of attending to minute details in familiar and strictly limited surrounding, and not to supernormal visual acuity.

Their sensory skills, in other words, were domain specific, narrowly specialized, and did not arise from an overall sensory superiority (in that way, much like Kish's echolocation and other domain-specific perceptual learning; see Seitz & Watanabe, 2005).

In the 1960s, an interdisciplinary team of anthropologists and psychologists set out to systematically test a wide variety of populations' susceptibility to optical illusions using a comprehensive cross-cultural research method (see Segall, Campbell, & Herskovits, 1966). The project was an example of "ethnology." In anthropology, ethnology was a broadly cross-cultural examination of a single facet of life in multiple groups, a form of analysis once common in the field but much less seldom pursued now that in-depth knowledge of a single culture, conveyed in "ethnography," is much more highly prized. Segall and his team found that some populations were not sensitive to even basic optical illusions, such as the Müller–Lyer illusion. In particular, South African miners and San adults (a foraging population), as well as Suku children (from what is now the Democratic Republic of Congo), demonstrated minimal susceptibility to the Müller–Lyer illusion. The finding prompted Segall and colleagues to argue that the illusion was conditioned by perceptual experience in "carpentered" environments; exposure to buildings with right-angled corners taught the visual system to perceive the Müller–Lyer diagram as implying three-dimensional space (Stewart, 1973). As McCauley and Henrich (2006) discuss, the implications of Segall and colleagues' work were largely disregarded by later theorists who held that sensory systems were cognitively "modular" and resistant to developmental influences (e.g., Fodor, 1984/1990).

Similarly, the publication of Berlin and Kay (1969) highlighted that the number of basic color terms varied significantly across languages; nevertheless, focal colors emerged in a clear pattern as the number of basic color terms increased across languages. Although some observers have taken the pattern of focal color preference as an example of a human "universal," in fact, the evidence is much more complex and interesting: Variation seems to emerge from a combination of human endowment and perceptual learning, leading to profound differences in color perception but not to unlimited flexibility.

Since the 1980s, the study of sensory experience has re-emerged strongly in anthropology, especially following the influence of David Howes, Constance Classen, Paul Stoller, Nadia Seremetakis, and Sarah Pink, but in a decidedly more humanist frame rather than the earlier cross-cultural ethnological and psychological projects (see Herzfeld, 2001; Howes, 2005). Although these anthropologists sometimes draw inspiration from early psychophysical work in our field, like that of Boas or Rivers, the new wave of sensory research is more immediately inspired by the media studies of oral and visual cultures of Marshall McLuhan, the structural–cognitive research of Claude Lévi-Strauss, interest in sensory studies in history and the humanities, and the symbolic and ritual studies of Victor Turner. Even so, close ethnographic experience often highlights cultural variation in forms of sensing: Alfred Gell (1995, p. 235), for example, noted that the Umeda became particularly alert to sounds and smells in the forest where sight was limited by dense underbrush. Edmund Carpenter found Inuit hunters had extraordinary visual acuity in their home environments, spotting distant people on low-contrast ice fields (1973, p. 36; cited in Ingold, 2001, p. 253).

Contemporary anthropologists of the senses have strongly criticized the assumption that sensory systems are unvarying across cultures, or that cultures will develop uniformly as "visual" or "oral," for example, with the spread of literacy or the growth

AQ: Please note that the cross-reference "Constance Classen (1997)" has not been provided in the reference list. Please provide reference.

of televisual media. As Constance Classen (1997) has suggested,

> The objective of the anthropology of the senses . . . is neither to assume that smell, taste, or touch will be dominant in a particular culture nor to assume that they will be marginal, but to investigate the ways in which *meanings are, in fact, invested in and conveyed* [emphasis added] through each of the senses. (p. 405)

This approach has led some anthropologists to point out that the five senses model that is dominant in Western folk conceptions is a cultural construction (see Howes, 1991, 2005). Kathryn Linn Geurts, for example, found during ethnographic fieldwork among the Anlo Ewe in Ghana that they did not divide sensory experience as Westerners did. Moreover, the Anlo Ewe placed a strong emphasis on balance and kinaesthesia, forms of proprioception that are frequently left out of Western accounts of the senses, and believed that there were links between one's sensory carriage and moral status (Geurts, 2002, especially pp. 37–69). Other anthropological research, likewise, has highlighted different relations of what David Howes (2005) calls "intersensoriality," "the multidirectional interaction of the senses and of sensory ideologies" (p. 9).

Although anthropologists interested in the senses have often been critical of approaches to culture that are overly discursive (see Porcello, Meintjes, Ochoa, & Samuels, 2010), they have sometimes adopted models of sense experience that, for want of better models, treat abstract modes of understanding as an analog for sense experience. For example, David Howes (1991) argues that the anthropology of the senses should explore "how the patterning of sense experience varies from one culture to the next in accordance with the meaning and emphasis attached to each of the modalities of perception" (p. 3). Although certainly this is true, "meaning and emphasis" are likely only two of the forces that shape different cultural ways of perceiving, and focusing on these conscious elements may distract from more practical and inchoate forms of sensory enculturation. These anthropological treatments of the senses as carriers of "meaning" also have been difficult generally to connect to new research about perceptual learning or variation in psychology or neurology, although I would argue that there are intriguing parallels between anthropological research on the senses and cultural neuroscience accounts of sensory variation.

One of those areas of parallel is a body of work on sensory enskilment inspired by James Gibson's ecological psychology through the work of anthropologist Tim Ingold (2000). Cristina Grasseni (2004), for example, in her research on cattle breeders and livestock judges in Alpine Italy, focused extensively on how they develop visual skills to assess animals in ways that were simply not recognizable to naive viewers:

> Skilled practitioners know well that bodily knowledge entails discriminating and disciplining the attention of the senses, including that of sight. Skilled vision implies an active search for information from the environment, and is only obtained through apprenticeship and an education of attention. (p. 13; see also Grasseni, 2007)

The "education of attention," a phrase borrowed from Gibson (1966, 1979), can, over developmental time, lead to the sorts of domain-specific perceptual learning that have been recognized in both anthropology and psychology for more than a century. Ingold (2001) proposed the "education of attention" as a more ecologically valid way of understanding cultural learning than the suggestion that a form of knowledge, such as a schema or symbolic system, is "transferred" whole from one individual's mind to another's. The more effectively individuals focus on sensory variables with crucial information, the more accurate and efficient they can be at extracting the information that they need, such as distance to an object from a pulse-to-echo gap when echolocating. As Ingold's account suggests, an instructor such as Kish encourages this development, not by transferring knowledge but, rather, by directing novices' attention to the most crucial sensory variables in the environment. This observation also coincides with evidence that shows that when learning a motor-perceptual skill, feedback is most effective when it concentrates not internally, or on the actions themself, but externally, on the consequences of correct technique for perception of the environment (see Wulf, 2007). That is, effective coaching focuses on what the novice should perceive, not making him or her more self-conscious of technique.

This model of sensory enculturation as an education of attention with long-term consequences for neuropsychological functioning when reiterated over developmental time coincides well with evidence emerging from cultural neuroscience and the study of perceptual learning (Hedden, Ketay, Aron, Markus, & Gabrieli, 2008; Sasaki, Nanez, &

Watanabe, 2010). Some of this research has noted differences between Western and Asian subjects in visual scene perception: Westerners tend to focus more on focal objects and neglect context, whereas East Asian subjects are more sensitive to contexts, relationships, and backgrounds in visual perception (Chua et al., 2005; Kitayama, Duffy, Kawamura, & Larson, 2003; Nisbett & Miyamoto, 2005). Simply stated, different modes of attending to scenes are habitual, and the styles of perception in which one engages most often become both more skillful and less effortful. For example, Goh and colleagues' (2007) finding that older Asian subjects showed less adaptation in object-processing brain regions compared to Western counterparts may be seen as demonstrating a different habit of perceptual behavior and the long-term consequences of reiteration of this pattern over the course of a lifetime. The focus on the education of attention also coincides more closely with models of cultural context as a form of priming (e.g., Lin, Lin, & Han, 2008; Oyserman & Lee, 2008). If "culture" is, in part, perceptual orientation to particular sources of sensory stimuli in an environment, then it makes sense that priming techniques can redirect that attention in particular situations, temporarily suppressing or exaggerating encultured sensory tendencies.

More important, considering sensory learning as a form of enculturation focuses our research question in a more limited way on the distribution of sensory skills. Currently, most cultural neuroscience research treats variation in sensory behavior as merely symptomatic of a grander cultural pattern, such as "holistism" or "analytic" thinking. Although this contrast certainly captures some intriguing differences, a *less* comprehensive, *less* all-encompassing model of culture allow us to better deal with exceptions to the overarching pattern (Oyserman, Coon, & Kemmelmeier, 2002). A sensory enculturation approach also coincides with a more sophisticated model of cultural variation as the result of slowly sedimented bodily practice (rather than internalized cognitive schema; see Kitayama & Uskul, 2011; Roepstorff, Niewöhner, & Beck, 2010) and possibly occurring throughout the nervous system, rather than just in late processing areas (e.g., Zenger & Sagi, 2002). A more diffuse and fragmented sense of culture additionally raises the possibility of recognizing many more forms of culture than are currently discussed in cultural neurosciences. Moreover, a focus on lower-level variation, such as sensory behavior, may offer entry points for dealing with psychological problems across cultures, such as differing patterns of dyslexia or the social–perceptual disruptions of autism spectrum disorders, by acknowledging how various forms of sensory learning might be differently disrupted by organic obstacles.

## The Culture Concept in Cultural Neuroscience

Most discussions of contemporary cultural theory note that anthropologists have long disagreed on how to define the term, dating back at least to the middle of the twentieth century when so many definitions of "culture" were on offer that Kroeber and Kluckhohn (1952) felt the need to collect more than 150 of them. Although some critics have pointed to this morass as a reason for abandoning the use of the term, I believe that "culture" has served valuably to highlight a broad area for investigation, one that is irremediably difficult to delineate precisely because of its theoretical and practical imbrication with various dimensions of human existence but also with elements often held to be its opposite. For example, if "culture" is opposed to "nature," the definition of "nature" itself varies across groups (and thus is "cultural") (see Descola, 2013).

The murkiness and variability of the term in anthropology arises in part from the sheer breadth of the phenomena that anthropologists wish to consider and the different forces that produce patterns of human variation. Although "culture" may suggest that this induced variation is patterned, and that it is not "innate," in fact we know that these too are contentious claims: Culture itself can be contested and shot through with coercion, and the very capacity for culture is itself a biological trait of humans. From the consequences of deeply held, collective cultural values or ideologies to the effects on individuals of patterns of face-to-face interaction and implicit norms, from the cognitive entailments of language diversity to the nonconscious influences of patterns of behavior or bodily training, and from particular products of universal cognitive mechanisms to the widespread influence of technology on those who use it—all of this (and more) has been considered "cultural." That is, anthropologists disagree about the definition of culture, in part, because the range of phenomena under discussion is simply so broad and rich. Culture is less an explanatory device than an empirical project.

In contrast, the definition of "culture" that dominates cultural neuroscience, especially that implied in the choice of research questions and subjects, seems much smaller, and it focuses not on understanding any individual culture but instead on documenting cultural difference. As Cohen (2009) writes, "A person reading these literatures could be excused for concluding that there is a very small number of cultural identities (North American vs. East or Southeast Asian), that vary principally on the dimensions of individualism–collectivism or independent–interdependent self-construal" (p. 194). The dangers of this treatment of culture, including a pattern of essentializing and binary thinking and elements that are inevitably missed, have been highlighted by other authors (Martínez Mateo, Cabanis, Cruz de Echeverría Loebell, & Krach, 2012; Martínez Mateo, Cabanis, Stenmanns, & Krach, 2013).

The basic impulse that motivates and orients cultural neuroscience, however, bears repeating despite the criticisms because it is so radical. As Denkhaus and Bös (2012) write, cultural neuroscience departs from more mainstream neurological and cognitive research in a crucial regard:

> While mainstream social, cognitive, and affective neuroscience implicitly or explicitly assumes that basic psychological processes and their neural correlates are universal, cultural neuroscience reckons with the cultural embeddedness, and hence with the particularity, of these processes. Cultural neuroscience thus challenges the universal applicability of findings derived from psychologists' and neuroscientists' preferred research subjects, European–Americans. (p. 436)

Although cultural neuroscience must contend with its own definitional problems and sampling biases (see Chiao, 2009), Denkhaus and Bös are correct that this basic project "at least put into question some rather uncritically held assumptions of mainstream neuroscience research: Cognitive processes are not simply hard-wired, but may be shaped by cultural contexts" (p. 437). This fundamental shift in the understanding of human nature warrants strong defense, especially given that disparities in health care may be exacerbated by unexamined biases in research that disproportionately focus on WEIRD populations (Henrich et al., 2010).

If anything, the first phase of cultural neuroscience research has been a more radical challenge to cultural anthropology than neuroscience because, even given the limits of sampling and theoretical issues, the first wave of findings in cultural neuroscience suggests that a divide between culture and biology cannot be sustained. This divide between mind and brain has been a crucial boundary for dividing intellectual labor and securing a space for cultural inquiry, so the erosion of the distinction has caused some anthropologists to fear that our biological colleagues will seek to swallow up entirely human variation in a wave of biological reductionism (e.g., Martin, 2000). In contrast, those of us interested in neuroanthropology perceive an extraordinary opportunity to expand the purview of cultural research and to recognize that culture has profound biological consequences, abundantly illustrated by pioneering efforts in cultural neuroscience. The "of-course-ness" of that realization now—the confidence we have that culture affects neurobiology—should not blind us to how radical the proposition appeared little more than a decade ago.

For neuroanthropology, however, the goal is not just to compare the neuropsychological performance of people from different ethnic groups, although this has served well as a proof-of-concept that such differences have neurological consequences. Rather, neuroanthropologists seek to use field-based, empirical research on naturally occurring human variation to better understand the brain, or even just to ask better questions about what is neurologically plausible (Domínguez Duque, Turner, Lewis, & Egan, 2010; Lende & Downey, 2012). This approach requires embracing the broadest possible sample of human variation because we will only know what these mechanisms are capable of by studying extremes. We will only understand how this variation can arise by examining the processes that produce pools of apparent continuity, but it also requires us to be open to multiple types of data, even if those data are only suggestive. To exclude considering cultural variation because its bearers do not reside close to neuroimaging laboratories or cannot be expressed by a subject who must remain horizontal and still inside a magnet is to too tightly leash our curiosity about human variation.

A possible remedy for some of the current issues with cultural neuroscience is not to abandon entirely the concept or to attack rhetorically one variant definition or another but, rather, to strongly encourage a more anthropological appetite for cultural variation, a broader curiosity about the uncanny weirdness and startling variability of humanity. The fact that this has not already happened highlights the fact that, despite frequent admonitions by cultural neuroscientists that they must draw on anthropological insight, references to anthropologists—except for a small core of theorists who talk about contrasts between the Occident and Orient at a civilizational level—in cultural neuroscience writing are surprisingly rare. The fault is not entirely with the cultural neuroscientists. As Theodore Schwartz (1992, p. 324) argued more than two decades ago, psychology and anthropology have undergone a "mutual estrangement" due to a fundamental "inter-paradigmatic misunderstanding," with fault for this gap "on both sides." For example, as I suggested in the survey of sensory research in anthropology, many in my field have moved away from precisely the sort of broad comparative perspectives provided by ethnology that might be most useful for refining questions in the cultural neurosciences. The revival of interesting cross-cultural research (e.g., Henrich et al., 2010) heralds greater potential scope for collaboration (see also Brown & Seligman, 2009; Seligman & Brown, 2010).

In particular, the dominance of East–West comparisons in the field of cultural neuroscience has starved the emerging speciality of research questions. Over and over, the theoretical framework of the research is predictable, the outcome foregone: a reiteration of independent–interdependent self theory or analytical–holistic thinking. On this particular cultural quality, we have increasing depth and sophistication, including the intriguing addition of genetics research and gene × culture interaction (Chiao & Blizinsky, 2010; Dressler, Balieiro, & dos Santos, 2012; for review, see Chiao, Cheon, Pornpattananangkul, Mrazek, & Blizinsky, 2013). But how do we go about opening up cultural neuroscience to new forms of cultural difference while still preserving the enormous advances made by the field thus far? I argue that being less concerned about the definition of culture and more curious about potential human variation no matter what form it takes will help us to understand both the processes that produce and the consequences of human neurological variation. Although the individualist–collectivist contrast between Western and Asian populations has served as an excellent proof-of-concept for a nascent cultural neuroscience, we run the risk of it constraining what we can learn, especially given the enormous challenges of human neurodiversity and health.

## Unleashing Culture

I disagree strongly with Peter Smith (2010, p. 91) when he suggests that "new directions" for cultural psychology (or neuroscience) should include a return to Geert Hofstede (1980) for more cultural "dimensions" to explore (see also Markus & Hamedani, 2007). The "dimensional" approach to the study of cultural–psychological variation can obscure as much as it reveals, and it makes the current study of culture in cultural neuroscience prone to the charge of "binarity" (see Martinez Mateo et al., 2013, p. 2). For example, the anthropological record includes many more variations of self-constitution than just Western individualism and East Asian collectivism, including variant forms of both. Kuserow's (2004) study of American individualism highlights that individualism varies across classes, with working-class communities favoring a "hard individualism" that prizes toughness, obedience, vigilance, and the ability to defend oneself, whereas upper- and middle-class communities demonstrate a "soft individualism," in which each individual's potential and uniqueness is privileged, and egalitarian social relations are expected even between parents and children. Arguably, the patriotism, consumerism, and precarious labor situations of many Americans might also generate situations in which they might express communitarian ideals or self-concepts, even though explicit ideology might prize individualism. Rather than just contrasting individual independence with interdependence, a more culturally curious research agenda would seek to exploit these variations, to create experimental conditions in which normally independent individuals might act otherwise. Priming experiments already do essentially this, but they tend not to use native situations to try to prime counter-stereotypical behavior instead of mapping out different forms of individualism, for example (Oyserman & Lee, 2008).

Similarly, collectivism itself may take different forms, not just the interdependence of identity based in family networks highlighted by Markus and Kitayama (1991). For example, hierarchical interdependence might contrast vividly in some experimental conditions with a more egalitarian, group interdependence, such as a contrast between Confucianism and Maoism. Again, prying apart competing tendencies, noting intergenerational variation, and finding situations in which behavior cleaved might produce a much more robust account of Asian interdependent self-conceptions, including within-group variation. Does identification with a clan totem, or a name-sake ancestor, or one's own prior reincarnations produce similar unusual effects in the neurological systems that subtend self-perception?

Anthropology records even more unusual variants of interdependent self (but see Spiro, 1993). Based on a wide ethnological survey of anthropological literature, Philippe Descola (2013) has outlined patterns of cultural variation in ontology—that is, fundamental schemas for understanding the relationship of humans to other living things. He argues that Westerners, including anthropologists, are "naturalists," assuming an absolute division between culture and the natural world and also between humans and other living things. In contrast, various other forms of identification and anthropomorphism are evident in other societies, including animism, totemism, and other variants. Under what experimental circumstances might individuals from these societies evidence profoundly different neurocognitive processes for imaging these rich connections with the natural world?

Similarly, Rane Willerslev (2004) explored the forms of identification that Siberian Yukaghirs hunters employ so that they may approach their wary reindeer prey; the hunters' sense of identification is so intense that they sometimes fear that they will slip their human form and join the animals that they hunt. Or what about individuals who undergo dissociative experiences in societies that encourage these states of awareness as a form of healing, such as in Brazilian candomblé (Seligman & Kirmayer, 2008)?

Although the logistics (or ethics) involved in designing experimental protocols may prevent us from using familiar neuroimaging techniques on indigenous populations, all the more reason that we should study neurodiverse populations close to home, such as echolocating blind activists or others whose skills or ways of living offer glimpses of the neurological mechanisms that might underwrite other forms of cultural difference. In fact, what differences might exist between university students in Western and Asian countries are likely at least partially arbitraged away by a host of shared experiences—literacy, urbanization, technology, mass media, consumerism, and shared popular culture. We should use our imaginations to slip the leash of any narrow comparison of independent and interdependent selves, to seek out the greatest neurocognitive variation possible, even close to home.

Research on highly skilled populations who demonstrate activity-dependent developmental neuroplasticity (e.g., Maguire et al., 2000) can also lead us to hypothesize about related cases of cultural variation, both near and far. For example, are the navigational skills of Pacific Islanders, discussed in such fine detail by Ed Hutchins (1995), underwritten by similar neurocognitive mechanisms as the urban geographical knowledge of London cab drivers? Or are the differences in their performance so great that they likely indicate a fundamentally different process of skill acquisition and target mechanisms in the brain?

A broader anthropological sensibility can expand cultural neuroscience, multiplying the target populations and questions. Differences in mean performance between one ethnic group and another, or between two linguistic communities, do not measure "culture"; they simply map out some portion of that possible variation (while simultaneously submerging other parts, such as within-group variation arising from behavior, habits, education, or other developmental patterning).

## Closing Gaps by Opening Horizons

In psychiatric anthropology, it is axiomatic that the prognosis for those with psychiatric conditions varies significantly across cultures, in part due to people's expectations about recovery, the ways that the healthy interact with those who have conditions, and the forms of treatment and support available in different cultural contexts. World Access for the Blind and the case of human echolocation highlights the way that "disability" emerges, not just from the entrenched characteristics of those with neurological and physiological anomalies but also from the way that these anomalies interact with the expectations and actions of others. To be blind is not merely to be bereft of sight. To be blind is, in part, to be forced to interact on unequal terms in an environment, created by those with different sensory abilities, that can be more or less hostile to one's limitations. To be blind is, in part, to engage with people who may be entirely ignorant of your potential, with consequences for the development of your sensory abilities.

Conditions such as blindness can be made more difficult precisely because those people who have them do not typically form "subcultural" groups in which they can interact with others like themselves, developing the forms of collective and cumulative knowledge that the rest of us (those who are "abled" or neurotypical) incorporate in the course of sensory education. To follow Daniel Kish or another one of the mobility instructors in World Access for the Blind is not merely to see individuals using their abilities; it is to observe the temporary creation of an environment in which their sensory condition is the norm and in which information about being in that world flows between people who jointly inhabit it. This makes their story an optimistic one, not merely about solidarity and decreased prejudice, but also in that neuroscientific and psychological research on diversity can directly affect the individuals who are the subjects of that research, in part by shaping their ability to self-reflect and refine their skills.

Cultural neuroscience and neuroanthropology have a crucial role to play in helping to facilitate communication among those who share distinctive neurological endowments but also between diverse groups who do not. A public aware of neurodiversity and the necessity of supporting diverse forms of development would be much more likely to encourage practices such as exploratory echolocation, recognizing the long-term consequences of enforced passivity on a developing child, sighted or blind.

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CHAPTER

# 4

# Health, Development, and the Culture-Ready Brain

Charles Whitehead

**Abstract**

This chapter aims to contribute to an improved understanding of the social brain and the rising tide of psychological health in children. It challenges certain misperceptions affecting scientific research and child-oriented policies, and it presents a "play and display" hypothesis that holds that spontaneous communication, play, and performance (social displays), uniquely developed in humans, are a major reason for our enlarged brains and are essential to the development of self/other-awareness, brain maturation, human culture, and healthy child development. The hypothesis is linked to pivotal theories in the social sciences, notably social mirror theory, ritual/speech coevolution theory, and the theory of anti-structure. Implications for child health are discussed, and the argument is supported by evidence relating to epigenesis, brain development, developmental psychology, paleoanthropology, neuroimaging research, and the culture-ready brain. The chapter concludes with some pointers for future child development policy.

**Key Words:** anti-structure, brain evolution, child development, culture-ready brain, epigenesis, neuroimaging, performance, play, social display, social mirror

## Introduction

It seems paradoxical that, despite the Decade of the Brain and the dramatic expansion of the cognitive sciences, psychological problems should be increasing, while scientists themselves cannot agree on the precise causes of these problems. Indeed, there is no scientific consensus on what makes the human mind, brain, and behavior unique (Henshilwood & Marean, 2003; Renfrew, Frith, & Malafouris, 2009); what human beings need for optimal development (Narvaez, Panksepp, Schore, & Gleason, 2012); or what kind of child-oriented policies are most likely to favor the development of happy, healthy, and socially positive citizens (Narvaez et al., 2012). One might question whether we really are living in an age of unprecedented self-knowledge or, perhaps, whether cognitive science is part of the problem rather than the solution. It is the aim of this chapter to challenge current understandings (or misunderstandings—see next section) and contribute to a better theoretical basis for defining human needs, guiding future research, and helping policy-makers to make more informed decisions.

## Some Common Misunderstandings

I think there are several misunderstandings that are of relevance to cultural neuroscience and health, especially mental health, and that are largely the result of ideological bias (Whitehead, 2010a, 2010b, 2012).

An obvious example is the Protestant work ethic—associated with the rise of capitalism and the industrial revolution (Weber, 1904–1905/1930)—resulting in an ethos that values work over play (Turner, 1982), object over social skills (Smith, 1988), science and technology over the arts (Jennings, 1990), and logic over imagination (Jennings, 1990). Here, evidence is presented that suggests we should reverse these valuations.

It is important to realize that human beings did not evolve to *work* in the modern economic sense. Work of this kind began with the agricultural revolution approximately 10,000 years ago (Gage & DeWitte, 2009; Mummert, Esche, Robinson, & Armelagos, 2011; Parikh & James, 2012), which is very recent in an evolutionary timescale. During the rest of our evolutionary past, our ancestors foraged for food as do all mobile animals. Work in the bureaucratic sense is even more recent, following the inventions of literacy and numeracy in the earliest river valley civilizations (Parkinson, 1963), whereas academic work *sensu stricto* is the most recent of all, associated with various schools of Asian and European philosophy—Hindu philosophy being the oldest. The first Western teaching institution was the Academy in Athens, founded by Plato in approximately 387 BCE.

The Protestant work ethic influences scientific research (Whitehead, 2008a) (see the section titled Social Displays in Human Development and Evolution and that titled The Culture-Ready Brain) as well as parental attitudes and government policies relating to child care, education, school recess, and the teaching of the arts (see Man-Made Maladies).

A second ideological bias is Western individualism (Whitehead, 2008b; Wood, 1972). The behavioral sciences, rightly, have moved away from individualistic approaches (Singer, Wolpert, & Frith, 2004), and cultural psychologists and neuroscientists have conducted considerable research on the mental and neurological differences between Westerners and Easterners—the latter having a more collective sense of self (Chiao & Ambady, 2007; Chiao, Li, & Harada, 2008). Nevertheless, there are still lingering consequences of individualistic thinking. For example, the social intelligence hypothesis (Chance & Mead, 1953) was proposed almost 40 years before Leslie Brothers published her social brain concept (Brothers, 1990). Although this concept has proved seminal, there is still a tendency to regard much of the human brain as "nonsocial" (cf. Adolphs, 1999, 2003). According to the social intelligence hypothesis, brain expansion in primates was driven by the cognitive demands of living in relatively complex social groups (Byrne & Whiten, 1988). This implies that any part of a primate brain that is expanded (relative to its homolog in a non-primate mammal of similar body size) is likely to serve one or more social functions. This applies to most of the human brain, including structures still regarded as nonsocial. The section titled The Culture-Ready Brain extends the social brain concept in directions that have been relatively neglected in the behavioral sciences (Whitehead, 2010c).

Individualism not only biases our view of the human brain but also underestimates the importance of cooperation in biology and evolution (Whitehead, 2012). Organisms are cooperating societies of organs, cells, organelles, etc. Similarly, genes must cooperate with genomes if they are to survive, and ecosystems are essentially mutualistic. Without cooperation, there could be no competitors, and cooperation is the more fundamental of the two. As in biology, so in education, where individualism leads to an excessive stress on personal excellence and competition (see Man-Made Maladies).

A third and very influential bias is genocentrism, which treats the "selfish gene" as the prime mover in evolution (Dawkins, 1989). This bias itself is in part a by-product of individualistic thinking with its emphasis on competition. Although the selfish gene approach has done much to improve understanding and dispel some former false assumptions, its claim to Darwinian legitimacy is questionable. In strict Darwinism, the prime mover in evolution is environmental threat. In the absence of threat, natural selection tends to *resist* evolutionary change. Furthermore, the selfish gene approach cannot explain the recurring patterns in macroevolution and the remarkable ubiquity of convergent evolution (see Epigenesis). Comparative anatomy (Thompson, 1917/1992) and fossil evidence (Young, 1981) suggest that evolution is far less random then assumed by genocentric thinkers such as Richard Dawkins (1989) and Stephen Jay Gould (1989).

A particular problem occurs when genocentric speculation imposes the pseudo-Darwinian concept of "memes" onto cultural evolution (Dawkins, 1989, pp. 189–201). Meme theory makes cultural phenomena—such as religion—the result of random copying errors, and thus arbitrary, and often—in the case of supernatural beliefs in particular—functionless or worse (Dawkins, 2006). This theory entirely overlooks the specific adaptations that make human beings capable of creating, maintaining, and developing culture of human type (Whitehead, 2012) and also the evident discontinuities between animal and human cultures (Whitehead, 2003, 2014). Ethnographic evidence does not support the view that religion has no function, and it has led many social anthropologists to conclude that ritual was essential to the origins of human culture and to its early development and remains today an important mechanism of cultural stability and adaptive change (see Theoretical Background). Later I address evidence that counters genocentric assumptions, and discuss specific human adaptations.

A fourth ideological bias is logocentrism—the attribution of such major importance to language that other fundamental differences between human and nonhuman apes are underestimated (Whitehead, 2014). In combination with genocentrism, this leads to false understandings of language evolution and human evolution more generally (Whitehead, 2003, 2014). Of particular relevance here is the way logocentric thinking conflates all kinds of social displays—including music and dance—under the rubric of "communication." Later, I sketch a typology of social displays and their development during childhood and evolution that makes clear how logocentrism fails to accommodate the richness and spontaneity of human social behavior.

A fifth bias is cognocentrism—the assumption that brain expansion during human evolution was primarily driven by selection pressure for "intelligence" (whether social or not) and that our most important mental processes are "cognitive" and therefore conform to an input → processing → output model derived from computing (Whitehead, 2010b). The following section includes an alternative view of brain expansion, and a later section reviews research by performative psychologists showing that human development is highly dependent on output-first behaviors (i.e., spontaneous behaviors that occur even in the absence of any external trigger).

Although the five tendencies mentioned previously do not constitute an exhaustive list, they are sufficient to make clear the motivation of this chapter and the evidence chosen to support its central thesis—the crucial importance of social displays and their relevance to cultural neuroscience and health.

## Theoretical Background

### *The Play and Display Hypothesis and Social Mirror Theory*

The "play and display" hypothesis holds that communicative, playful, and performative behaviors (social displays) are uniquely developed in humans, are the core of what makes us human, were major factors driving brain evolution, are crucial epigenetic mechanisms that sculpt individual brains, are fundamentally constitutive of human culture, and are absolutely essential to healthy child development (Whitehead, 2001, 2003).

The hypothesis is a corollary of social mirror theory, first proposed at the end of the nineteenth century by Wilhelm Dilthey (1883–1911/1976) and James Mark Baldwin (1894/1902) and further developed in social psychology by George Herbert Mead (1934/1974); in sociology by Erving Goffman (1959); in anthropology by Victor Turner (1982); and in developmental psychology, paleoanthropology, and neuroscience by Charles Whitehead (2001, 2003). Social mirror theory holds that "mirrors in the mind require mirrors in society" (Whitehead, 2001). That is, social displays make experiences public and salient so that, during childhood, we begin to notice them in ourselves and others and become aware that we and others have such experiences. As G. H. Mead noted, this theory rejects Western individualism and its expression in Cartesian solipsism—*cogito ergo sum* should read *cogitamus ergo summus* or even *sensoramus ergo summus*. Social mirror theory makes reflective consciousness—the ability to read one's own mind—and the ability to read other people's minds a singular inseparable phenomenon.

### *Ritual/Speech Coevolution Theory*

Social mirror theory complements a second theory, originally proposed by Émile Durkheim (1912/1964), that the emergence of language—and culture of human type—depended on ritual. What distinguishes language from animal communication, Durkheim argued, is displaced reference—the ability to refer to things not present in the here and now but only in the mind of the speaker. How can we encrypt an intangible, he asked, unless it is first made public by ritual pantomime—a conventionalized drama that everyone understands and that is "sacred" in the sense that it carries the consensual authority of an entire community?

Speech–act theorists have advanced a second argument that points to the same conclusion (Austin, 1978; Grice, 1969; Searle, 1969). Words are cheap, and it is too easy to lie. If language could not be trusted, it would simply be ignored, and so have no function. Hence, language depends on a "social contract" (i.e., a communally imposed code of behavior with reasonable guarantees of honesty). In societies without police or judiciary, this can only be implemented through ritual and ritually constructed supernatural beliefs (Knight, 1998).

There is a third argument that also points to a ritual origin for language, although this was denied by its eccentric author, who deemed ritual unworthy of scientific interest. Lévi-Strauss (1950/1987) was greatly intrigued by the curious fact that, in animistic societies, words such as *mana, wakan*, and *orenda*—commonly translated as "medicine" or "sacred power"—also function as empty referents. That is, like "something" in English, they can be used to denote anything new, strange, or for which no other word can be found. He inferred a single big-bang origin for both language and religion (as well as culture of human type). In that primal creative moment, "the entire universe all at once became *significant*" (p. 60). In his view, the first utterance would refer to this cosmic significance and then, as later words were differentiated from this mother-of-all-words, the residual signifier would continue to refer to the prime mover in creation *and* everything not yet included in our referential system of meanings.

Anyone familiar with religious experience research, as pioneered by William James (1902/1985) and Alister Hardy (1979), will recognize this "entire universe all at once became significant" as a classic feature of spiritual experience. Even in the secular West, between a third and a half of the population has had at least one spiritual experience (Wulff, 2000). However, spiritual experiences are much more widespread and frequent in foraging communities (Bourguignon, 1973). Indeed, it is difficult to see how words such as *mana, wakan*, and *orenda* could have acquired their significance in any other way. It should not surprise us if language (and human culture) did originate in an "altered state."[1] Such states are an inevitable consequence of human dissociative or hypnotic abilities (Bliss, 1986; Tart, 1969) and, among hunter–gatherers, virtually all innovations—new dances, new customs, and even new fish traps—derive from dreams, visions, ritual trances, or divine visitations (for review, see Whitehead, 2011). Foraging communities (which value the archetypal over the creative, and tradition over "progress") accept such innovations only because they are regarded as gifts from the supernatural realm.

Durkheim's argument regarding the ritual origins of language has never, to my knowledge, been effectively disputed, and it has been widely influential in social anthropology. His idea has been extended to become ritual/speech coevolution theory (Enfield, 2010; Knight, 1998, 2014; Lewis, 2009; Power, 1998, 2014; Rappaport, 1999; Watts, 2009, 2014; Whitehead, 2014). In its current form, the theory further maintains that any attempt to explain language as an isolated trait is akin to explaining the emergence of the credit card without considering the preconditions on which credit cards depend—such as commerce; money; banking; the digital computer; and the means to deter, detect, and punish fraud. It is therefore impossible to "explain" language evolution as a singular adaptation distinct from human culture. Language is a part of human culture, and the entire package has to evolve (or be invented) as a whole.

Ritual/speech coevolution theory complements social mirror theory because it recognizes that mental insight requires mental states to be made public, and because ritual itself is a social mirror—a social display dependent on other social displays, most notably pantomime or role-play but also commonly song, dance, visual art, and so on. Hence, culture of human type is dependent on the social displays discussed later.

### *The Theory of Anti-Structure*

There is a third theory that, like the play and display hypothesis, is derived in part from social mirror theory. This is the theory of anti-structure. The theory began with a 2-year study of rituals in India by Arnold van Gennep (1909/1960). Van Gennep argued that all rituals are "rites of passage" because they accomplish transformations—whether in individuals or groups of similar individuals ("life crisis rites" such as birth, initiation, marriage, and funeral rites) or in society as a whole ("calendrical rites" such as New Year, Halloween, or Sunday communion). He further claimed that all rites of passage comprise three phases—a separation phase, in which participants are taken out of their everyday world; a transitional phase, in which transformation is accomplished; and an incorporation phase, in which participants are returned to the mundane world transformed. Most important, he observed that the transitional phase was characterized by suspension or violation of everyday norms (mainly in life crisis rites) or by a Saturnalian inversion of everyday norms (mainly in calendrical rites). For example, in the latter case, incest or cannibalism, normatively regarded as abhorrent, may become sacraments in ritual. Christian communion is an

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[1] This idea was first proposed in my MSc dissertation (Whitehead, 1995) and is based on Turner's (1969) theory of anti-structure and the observation that the transformative power of ritual depends on collapse or inversion of everyday categorical distinctions. Such anti-structure is equally characteristic of altered states of consciousness, including ritual trance.

example of make-believe cannibalism as a sacrament, although actual cannibalism may occur, as among the Avatip (Harrison, 1993).

Victor Turner (1969, 1982) coined the term "anti-structure" to refer to the topsy-turveydom of the transitional phase in ritual. His theory of anti-structure holds that human life alternates between the structural role-play of everyday life and the anti-structural role-play of ritual, recreation, and the arts. He noted that there are many behaviors other than ritual that have anti-structural characteristics and serve transformative or restorative functions. For example, childhood pretend play, like ritual, takes place in a "transitional space" (Bateson, 1955; Huizinga, 1955; Turner, 1982; Winnicott, 1974), in which major developmental changes and enculturation are accomplished. Pretend play creates a shared imaginary world in which normative constraints do not apply and experimentation can take place without incurring real-world risk (and, of course, ritual itself involves an institutional form of pretend play). In secular industrialized societies, Turner (1982) observed, the functions of ritual have been largely taken over by recreational activities, entertainment, and the aesthetic arts. He further maintained that human societies depend on anti-structural episodes to maintain, repair, and revitalize social order and to accomplish cultural change when circumstances so demand. This is a far cry from the idea of random copying errors in memes.

Psychological theories of creativity show close parallels to the theory of anti-structure, invoking disorderly, nonrational, or playful processes—creative chaos (Cooley, 1902), daydreaming (Freud, 1907/1989; Baird, Smallwood, Mrazek, Kam, Franklin, & Schooler, 2012), cognitive synergies (Apter, 1982, 2008), REM sleep (Walker, Liston, Hobson, & Stickgold, 2002), divergent thought (Wade & Tavris, 2008), conceptual blending (Fauconnier & Turner, 2008), and so on. Otto Rank (1932/1989) described creativity as an "assumptions breaking process," and Michael Apter (1982) advanced a "theory of psychological reversals" that contrasts goal-directed thought (*telic*) with playful thought (*paratelic*). Apter notes that the former cannot arrive at anything new because linear reasoning always remains trapped within its own premises. Playful thought, in contrast, conflates categorical oppositions and follows multiple nonrational paths, so leading to serendipitous discoveries—novel ideas and concepts that could never have been predicted from a set of fixed assumptions. Great ideas are never products of logic but generally come "out of the blue" when not thinking purposefully at all—famous examples being Archimedes in his bath, Kekulé in his reverie, Newton dozing when he saw the apple fall, and Einstein imagining himself astride a ray of light traveling away from the town hall clock. Dreaming and daydreaming may be essential aids to scientific insight.

There is a certain inevitable logic to the theory of anti-structure. For example, to turn a caterpillar into a butterfly, there has to be a separation phase (pupation), an anti-structural transformative phase (the caterpillar body breaks down to be rebuilt to a new body plan), and an incorporation phase (the butterfly emerges from the chrysalis). Comparable processes are necessary even in town planning, where buildings may have to be demolished or modified, and a case could be made for sleep and dreaming as anti-structural processes with restorative and transformative functions. Indeed, anti-structural phases may be essential to all self-ordering systems that need to overcome their own internal entropy and adjust to changing environmental demands.

### *Conclusion*

The theories outlined here, taken together, implicate social displays (as defined later) in the coevolution of the human brain and self/other-awareness; the emergence of human culture (including language and religion); healthy child development; the healthy functioning of the human mind, human societies, and human cultures; creative thinking; and adaptive psychological and cultural change. The theory of anti-structure in particular has a degree of logical inevitability that makes it more like a theorem than a theory; that is, like Darwin's theory of natural selection, certain claims of the theory can be proved logically and cannot be disproved empirically because the empirical evidence must conform to whatever is logically inevitable. Later, I further explore the idea of logical inevitability in the contexts of epigenesis, child development, and evolution.

If the theories reviewed here are sound, then any research or theorizing in the relevant sciences, or policies regarding relevant aspects of civil society, that do not take these factors into account will be at best insufficient and at worst may have damaging consequences for human health, well-being, and social order.

## Man-Made Maladies

It has often been argued that because we no longer live in our environment of evolutionary adaptedness (Bowlby, 1951), we create for ourselves multiple problems of health, social relations, well-being, child development, and so on.[2] It has been further argued that the mismatch between human needs and the human-made environment has increased in recent decades, causing a rise in psychological problems such as autism, attention deficit hyperactivity disorder (ADHD), anxiety, and depression, as well as physical conditions such as obesity, diabetes, and autoimmune disorders (Narvaez et al., 2012). Darcia Narvaez and colleagues claim that human development is being misshaped by government policies, social practices, and public beliefs that fail to consider basic human needs. These authors argue that practices such as breast-feeding, co-sleeping, and parental social support have waned in modern society, with adverse consequences for our children. One of these authors, Jaak Panksepp (2008), specifically links the rise in ADHD to diminished opportunities for natural play in modern societies, pointing out that psycho-stimulants such as Ritalin—increasingly prescribed for modern children—suppress playfulness and so, perhaps, compound rather than resolve the underlying problem.

Compared to the 1970s, children now spend 50% less time in unstructured outdoor activities (Juster, Stafford, & Ono, 2004). Children aged 10–16 years now spend, on average, only 12.6 minutes per day in vigorous physical activity—yet they spend an average of 10.4 waking hours relatively motionless (Strauss, Rodzilsky, Burack, & Colin, 2001). Opportunity for recess in many schools is also declining, even though children who have more recess are better behaved and learn more (Barros, Silver, & Stein, 2009). The American Academy of Pediatrics (2007) links increases in depression and anxiety to a lack of unstructured playtime. Children who are poor and black are the most likely to be denied recess. First-graders in high-poverty schools are 4.5 times more likely to have no recess at all as those in wealthier communities, and first-graders in high-minority schools are 7 times more likely to have no recess as children in mostly white schools (National Center for Education Statistics, 2005). The *Cambridge Primary Review* (Alexander et al., 2009) found that poverty was by far the greatest problem faced by children, and that homework in primary schools further disadvantaged children from underprivileged or unsupportive families. Furthermore, cutbacks following the recent recession have led to reduced time for arts education in schools. The performing and cultural arts are rooted in spontaneous behaviors related to play, as I hope to show, and this too is likely to have adverse psychological and social consequences.

In addition to ADHD, there is also a link between play, social awareness, and autism (Happé & Frith, 1996). That is, autistic children are deficient in both pretend play and mentalizing ability, and because make-believe play precedes the development of mentalizing, it may be the more fundamental deficit. Whether or not autism is indeed on the rise is a controversial issue, and a meta-analysis of epidemiological surveys failed to reveal disparities between different communities, nationalities, or ethnic identities (Elsabbagh et al., 2012). This may be due to lack of evidence rather than lack of difference. Some authors have disputed the claim that autism does not vary among races, citing a low incidence of autism in many Latin American countries (e.g., Peru, Argentina, Brazil, and Venezuela) and in several developing countries (e.g., Kenya, India, and Hungary) (Sanua, 1981a, 1981b, 1984). Sanua hypothesized that autism is more prevalent in Western, highly technological countries, where the nuclear rather than the extended family is predominant. American studies of schoolchildren and students consistently show a lower incidence of autism among Hispanics and First Nations people (Table 4.1; Dyches, Wilder, Sudweeks, Obiakor, &

**Table 4.1. Percentage (Based on Estimated Resident Population) of Students With Autism Aged 6–21 Years Served Under IDEA, Part B, During the 1998–1999 and 1999–2000 School Years**

| | Percentage of Students | |
|---|---|---|
| **Population** | **1998–1999** | **1999–2000** |
| Hispanic | 0.06 | 0.06 |
| First Nations | 0.06 | 0.07 |
| White | 0.08 | 0.1 |
| Asian/Pacific Islander | 0.1 | 0.12 |
| Black | 0.12 | 0.14 |
| Average among races | 0.09 | 0.1 |

Source: Based on data from Dyches et al. (2004).

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[2] The word "Man" in the heading to this section is perhaps justified because the maladies discussed developed or were exacerbated in patriarchal societies.

Algozzine, 2004). This may reflect differences in parental awareness, access to medical facilities, and likelihood of diagnosis. However, such factors would hardly explain why, relative to the American white population, autism is more prevalent among American Asian and American black populations.

In addition to the loss of freedom to play, there is a relentless pressure on British and American children to strive for excellence and competitiveness. The UK government, after commissioning the *Cambridge Primary Review* (Alexander et al., 2009), rejected its findings out of hand. The review described the National Curriculum proposals for England as "educationally unsound and evidentially questionable. . . . They perpetuate some of the most damaging aspects of current and past arrangements."

The report recommended re-empowerment of both teachers and children, more emphasis on arts and humanities, more outdoor lessons after the Scandinavian model, no homework in primary schools, and no formal education before the age of 6 years. Against all the available research and advice, the UK Department for Education is determined to begin academic education in nursery schools (Office for Standards in Education, Children's Services and Skills, 1999) (referred to by the press as the "nappy curriculum"). Something far more than the Protestant work ethic is needed to explain such obduracy—perhaps alarm at the increasing rate of PhD production in China, which threatens to overtake even the United States (Xinhua News Agency, 2002).

Paradoxically, current policies seem more likely to stunt academic achievement while unwittingly teaching underprivileged or less academically able children that they are failures with no place in today's society. The potential for alienation is inestimable. The *Cambridge Primary Review* comments, "Those who feel a failure are more likely to team up with the class tearaways to gain at least some affirmation, if, indeed, they are able to make friends at all" (Alexander et al., 2009).

In summary, it would seem that, in the United States and United Kingdom at least, biases such as the Protestant work ethic and Western individualism, in combination with political anxieties and parental concerns over child security, are conspiring to rob children of their necessary play and creative opportunities. This in turn hampers normal child development, limits educational achievement, adds to the social burden of psychological problems, and leads to social problems such as alienation. I submit that there is an urgent need for policymakers to revise their priorities, placing more emphasis on play and the creative arts.

## Epigenesis

Cultural neuroscientists investigate the relationships between genes, the brain, and culture. The authors of the chapters in this book are further exploring the relationships of these factors to health and health disparities. However, because of the genocentric bias mentioned previously, it is worth noting some cautionary points regarding the role of genes versus epigenesis in the development of the human brain and social behavior.

The term "epigenesis" usually refers to processes that alter gene expression or cell type, without change to the underlying DNA. Childhood play is itself an epigenetic factor in this sense. Jaak Panksepp and colleagues (Burgdorf, Wood, Kroes, Moskal, & Panksepp, 2007) have shown, in animal studies, that play has important effects on gene expression. Of 1,200 genes monitored, almost one-third exhibited significant changes in the degree to which they were transcribed. Panksepp (2008) observes,

> The key to human psychic development may lie in a combination of evolutionary tools and epigenetic programming. It appears that epigenetic programming from real experiences in society, culture, and the world in general molded *higher* brain regions much more so than the information encoded in genes. (p. 57)

However, I wish to extend the meaning of epigenesis to include factors that influence the evolutionary selection as well as the expression of genes—namely Platonic factors and emergent phenomena, which have more to do with logical inevitability than with physiology.

A simple example of an emergent phenomenon occurs when you stack oranges on a stall (Figure 4.1). The oranges inevitably form a mathematically ordered pattern—and it has nothing to do with genetics or even the laws of physics. Cigarettes in a pack form the same pattern (you might say that this is a primitive example of "convergent evolution"). Mathematical or Platonic constraints apply to just about everything that exists (Penrose & Clark, 1994). In 1528, Albrecht Dürer observed that you can change one head shape into another by a simple mathematical transform (Figure 4.2), and this in part inspired D'Arcy Thompson's classic work, *On Growth and Form* (Thompson, 1917/1992). He showed, for example, that genetically unrelated fish—even from different genera—can have

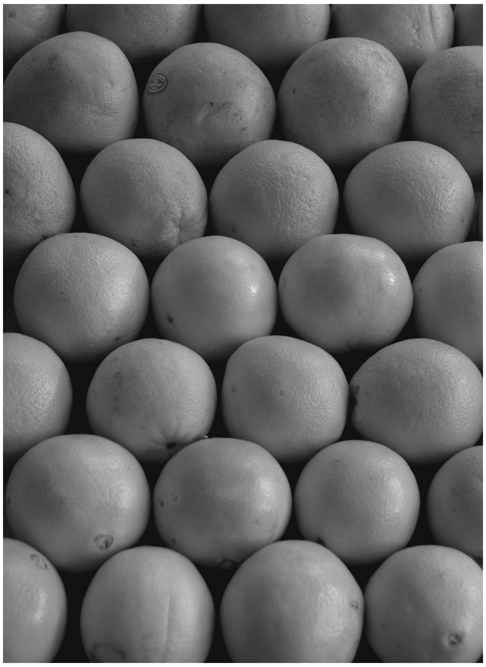

**Figure 4.1** Stacked oranges.

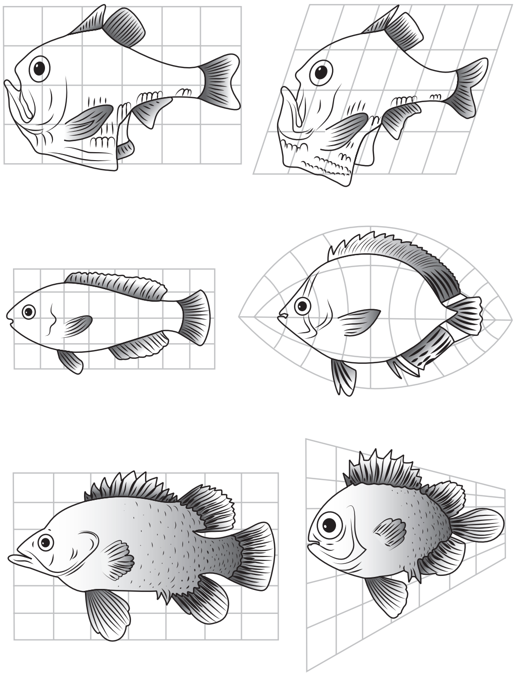

**Figure 4.3** D'Arcy Thompson, 1917.

bodies that are simple transforms of each other (Figure 4.3). Thompson's central argument was that biologists were overemphasizing natural selection and underemphasizing "Platonic selection"—the mechanical, mathematical, and physical constraints that determine biological forms (he was probably the first to point out the deficiencies of genocentric thinking).

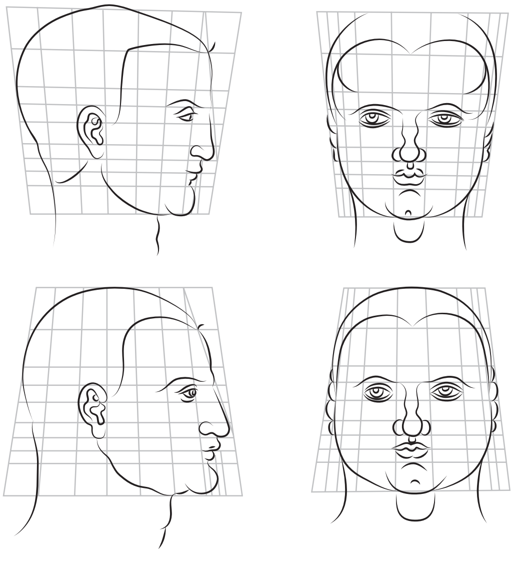

**Figure 4.2** Albrecht Dürer, 1528.

Convergent evolution illustrates a similar point. J. Z. Young (1981) observed that convergence is the norm rather than the exception in evolution. He gives a wealth of examples, including the wide range of placental mammals that have remarkably similar counterparts among marsupials (p. 582). Thus, relatively closely related animals may have very different phenotypes, whereas more genetically distant ones may be almost identical. This has nothing to do with genetics but, rather, with logical design solutions. Darwin (1839) observed convergent evolution among Galapagos finches, but some biologists view evolution as random and arbitrary (e.g., Dawkins, 1989; Gould, 1989). It would seem that Aristotle's "final causes" (*Historia Animalium* 350 BCE, translated by D'Arcy Thompson, 1910) are not so wrong as the randomizing Darwinians might think.

The "selfish gene" approach fails to explain the phenomena of macroevolution, such as the proliferation of new species and genera that follows (often exceeding in scale) the mass extinctions that end geological epochs (Young, 1981). The number of animal phyla, however, remains remarkably constant (Levinton, 1992). The Cambrian explosion saw the "simultaneous" (in a geological timescale) emergence of all known animal phyla that readily fossilize. Even the number of classes (the taxonomic group below phyla) has changed little compared with the creativity of the Cambrian. Following each mass extinction, all the same phyla reappear like risen ghosts. Adopting a D'Arcy Thompson perspective, one might surmise that this may be due to some kind of origami—there may be a fixed number of ways that sheets of cells can be folded to produce viable animal bodies. If so, then wherever animals evolve on earth-like planets, you would expect to find the same phyla, even though their genomes would be very different. Biologists have ridiculed Hollywood for creating human-like extraterrestrials, but any being capable of advanced technology may well be very like us—anatomically and psychologically.

The "take-home message" from this discussion of epigenesis is simple: Genes alone do not determine body plans or behavior, and—especially in the human case (discussed later)—the relationship between genes, brains, and behavior is seldom simple and direct. Genes exert effects on multiple anatomical and behavioral traits, and traits may be influenced by multiple genes. Hence, there is no such thing as a "good" or "bad" gene—innumerable epigenetic factors may determine how or whether a gene is "used" in the development of an adult phenotype.

Thus, for example, the empirical fact that the human *FOXP2* variant is essential for normal language development (Lai, Fisher, Hurst, Vargha-Khadem, & Monaco, 2001) does not imply that it is a "language gene" or a gene "for" language. The further fact that Neanderthals possessed this gene (Krause et al., 2007) does not imply that they had language (Benítez-Burraco, Longa, Lorenzo, & Uriagereka, 2008). According to at least three theories mentioned previously, they would also need ritual and/or a social contract, and it seems most unlikely that such cultural institutions could evolve exclusively by genetic means. There may or may not be genes "for" language, but the language people speak is determined by the community in which they are raised and not by their genotype. The architecture of the human brain is likewise not exclusively determined by genes, as explained in the next section.

## The Self-Sculpting Brain

### *Arborization and Pruning*

Jaak Panksepp (2008) notes that mapping the human genome led to a surprising discovery. Previously, many scientists assumed that the complexities of the human mind and brain must require a vast number of encoding genes to specify all of that data—possibly 100,000. Today, we must accept a more modest number—commonly estimated at approximately 22,000 (Panksepp, 2008). This is not much more than the genome of the mouse. It would seem that the differences between human and mouse minds and brains require very little in the way of genetic programming, and that the human mind and brain must be *underdetermined* by genes. This can be understood when we consider how brains are formed. Human genes need only to specify a broad anatomical plan and a general principle of synaptic proliferation (arborization) followed by pruning of both synapses and neurons. The developing brain then structures itself through its own embodied behavior—strengthening connections that are frequently used and pruning away those that are not (Shore, 1997).

An extreme example of such epigenetic influence is seen in children suffering severe emotional and sensory deprivation neglect (Erickson, Egeland, & Pianta, 1989; Gaudin, 1999; Helgeson, 1997; Perry & Pollard, 1997; Perry, Runyan, & Sturges, 1998). The brains of such children do not grow to a normal size, and due to pruning of unused networks, there may be severe cortical atrophy. Brain tissue is metabolically and nutritionally expensive (Aiello & Wheeler, 1995), so if you do not need a large brain, you are better off with a smaller one. You might say that the diminished brains of neglected children are well adapted to a life of sensory deprivation in a world without love—at a terrible cost to the individual, of course. Teicher (2000) comments, "Our brains are sculpted by our early experiences. Maltreatment is a chisel that shapes a brain to contend with strife, but at the cost of deep, enduring wounds" (p. 67).

There are two main "waves" of synaptic proliferation and pruning (Giedd et al., 1999; Huttenlocher & Dabholkar, 1997; Perrin et al., 2008):

1. The first begins before birth. The most rapid spurt of synaptogenesis occurs between 18 months and 2 years, followed by a period of extensive pruning. The greatest change in brain structure occurs between the ages of 2 and 5 years.
2. The second begins just before puberty, with the most intense branching and connecting at approximately age 11 or 12 years. Subsequent pruning begins to tail off at approximately age 15 years, but it continues throughout life. Maturation of the frontal lobes in particular is not complete until the early 20s.

The first wave might be understood as the phase in which the brain adapts itself to the universal norms of human sociality; the second as the phase in which the brain adapts itself to the culturally variable complexities of adult life. This may help to explain why formal education before the age of 6 years tends to be deleterious (Alexander et al., 2009). During the first phase of brain sculpting, children—motivated by the impulse to have fun—know what to do, whereas adults manifestly do not. In the second phase, children and adolescents need all the help they can get, and this is the phase in which formal education is essential in complex modern societies.

### *Adaptations of Human Childhood*

Human childhood differs from that of other primates in two important ways. First, human babies exhibit *secondary altriciality*. Many primates have altricial babies—that is, relatively helpless infants that require maternal nurture and care and have to be carried by their mothers until they are able to move independently with less risk of injury or predation. Altriciality is the converse of precociality, as seen in many herbivorous mammals, where the young have to run with the herd soon after birth. *Secondary altricialty*, however, means not only that babies are born in an underdeveloped state but also that rapid brain growth continues after birth. This phenomenon is known only in humans. In contrast to other apes, human brains at birth are only approximately one-fourth of their adult size, which means that 75% of brain growth occurs outside the womb. This is an evolutionary compromise between efficient bipedal locomotion (which requires a narrow pelvis) and possession of large brains (which requires a wide birth canal) (Walker, 1993). Despite this problematic compromise, giving birth is a dangerous time for mothers and babies, requiring the assistance of a midwife in most human communities.

Second, the human growth curve is slowed to provide an extended period of childhood, followed by an adolescent growth spurt. Chimpanzees also show such an "S"-shaped growth curve, but childhood is much more extended in humans than in chimps. The adolescent growth spurt, however, is equally rapid in both species (Rice, 1997).

Taken together, these two factors mean that human brains, relative to ape and all other known brains, have a massively expanded window of opportunity for self-sculpting through child and adolescent behavior.

## Social Displays in Human Development and Evolution

To understand what behaviors are important for the self-sculpting brain, we have to examine the things that children do spontaneously.

Obviously, newborn babies are able to cry and regularly do so. Psychologists might question whether this is really emotional communication or a reflex associated with the onset of breathing. However, very soon after birth, babies do express a number of basic emotions, so they are able to communicate at this primary level (Trevarthen, 1998).

Only 30 minutes after birth, they can also mimic the facial expressions of others (Trevarthen & Reddy, 2007; cf. Meltzoff & Moore, 1977, 1983). This is the beginning of contingent mirror play, which means that, for example, if the baby gurgles, the mother gurgles back; and if the mother sticks out her tongue, so does the baby. This is not mere mimicry, as assumed in simulation theory (Gallese & Goldman, 1998; Harris, 1991); babies will initiate such games themselves and express disappointment if their mothers do not respond (Trevarthen, 1974). By 6–8 weeks, this kind of play develops into "proto-conversational exchanges" which have the form and structure but not the content of linguistic conversation (Trevarthen, 1974).

At approximately 3 months, babies begin to express melodic vocalizations synchronized with balletic limb movements—the beginning of "song-and-dance" display (Beebe, 1982; Trevarthen, 1995). By 6 months, they engage in "clowning, tricks, and jokes" (Dunn, 1991; Reddy, 2001; Trevarthen, 1995), and by 9 months, they make marks on any surface—with pens, jam, or feces (Jennings, 1990).

So we can see that, within the first 9 months, babies have begun to express three distinct kinds of social display—communication, play, and performance—that have quite different functions:

1. *Communication* is goal directed and manipulative (Krebs & Dawkins, 1984).
2. *Play*, in contrast, although it has exploratory and developmental functions, has no goal—it is pursued "just for fun" (Apter, 1982, 2008; Bateson, 1955; Huizinga, 1955; Jennings, 1990; Turner, 1982).
3. *Performance* combines the functions of communication and play, and adds two more: grooming and entrainment. Grooming is the major means of bonding among primates, although humans have many more grooming

methods than do other apes (Whitehead, 2001, 2014). By "entrainment," I mean synchronization or coordination of bodily and mental behavior between individuals—ensuring that all are "singing from the same hymn sheet" or "dancing to the same tune." Together, grooming and entrainment enable two or more "selfish individuals" to behave like one much bigger selfish individual (Whitehead, 2001), as in Maori *hakas* or Nurenberg rallies and the like, which can be pretty daunting. Synchronized "song" and "dance" displays in dolphins (Connor, 1992) and gelada baboons (Richman, 1978, 1987) serve similar grooming and entrainment functions, and in the case of dolphins also serve to threaten or dominate others.

I call these early displays "implicit" because they involve primary intersubjectivity—referring to nothing outside the relationship between self and other (Trevarthen, 1979). Implicit displays deal with feelings, emotions, and bodies (e.g., laughing, crying, song-and-dance, and what Panksepp [2008] refers to as "rough-and-tumble play"). This buildup of implicit displays leads to the first of two major developmental watersheds that have no apparent parallel in apes and are accompanied by significant changes in the brain. Trevarthen (1995) refers to this first transition as the emergence of the "child as participant," whereas Baron-Cohen (1995) attributes it to the onset of the "shared attention monitoring mechanism." It marks the transition from primary to secondary intersubjectivity and the perception of self and other as social participants (Table 4.2). The baby now realizes that she and mother can pay shared attention to an object of common interest (Trevarthen & Hubley, 1978).

This new level of social awareness is followed by a new mode of social displays—projective mimesis (Jennings, 1990; Trevarthen, 1995; Whitehead, 2003, 2014). Mimetic displays are under voluntary control and are invented to order by the child (Burling, 1993). Mimesis should not be confused with mimicry (unreflective copying) or imitation (copying with insight into the goal of an action). Mimetic behaviors are not copied from other persons but, rather, represent things, sounds, actions, etc. by resemblance (Burling, 1993; Donald, 1991). For example, a child may represent a helicopter by swiveling one hand above the other or a police siren by making the sound "Nee-naw, nee-naw." Iconic gesture-calls of this kind emerge at approximately 12 months, roughly coinciding with the onset of projective pretend play (Trevarthen, 1995; Whitehead, 2003, 2014)—playing with toy objects that represent real objects. Such mimetic displays are referred to as "projective" because they project an idea—a thought, concept, or percept—onto an object or gesture "out there," in the world outside the mind.

Self-awareness continues to develop, with mirror self-recognition at 18 months (Gallup, 1994), along with new expressions of self-consciousness such as coyness and embarrassment (Parker, Mitchell, & Boccia, 1994). Thus, implicit displays are not *replaced* by mimetic ones. They serve different functions (affective and ideational) and continue to develop in parallel.

Performance, too, is developing. Babies take a lively interest in books with bold pictures—virtually as soon as they are able to sit up on their mothers' laps (the onset of secondary intersubjectivity; Trevarthen & Hubley, 1978). This may link to the development of their own mark-making behavior (implicit performance). But during the second year, it becomes clear that infants can read the pictures they are looking at (Jolley, 2010), even in the case of cartoons that bear little resemblance to their referents (Jennings, 1990; Jennings & Minde, 1993). For example, a child may pat a picture of a kitten, or try to "blow out" a cartoon flame. In a longitudinal study of two infant–mother dyads, infants aged 12–15 months—as yet unable to draw for themselves—regularly asked their mothers to draw for them, and by 18 months they would suggest subjects to be drawn (Yamagata, 1997).

These developments in displays lead to the second major transition—the "terrible twos" (Lewis, 1994) and the self-perceived in terms of social value (Table 4.2). Until this age, infants are relatively passive, generally allowing parents to wash, dress, or change them as they wish. But the terrible 2-year-old expresses his or her newfound autonomy and self-worth by resistance and rebellion.

Again, as with the first major transition, this new level of social awareness introduces a new mode of display: introjective mimesis. That is, in contrast to projective mimesis, which projects an idea "out there" into the world, introjective mimesis involves an identification of one's own body or mind with what is being represented. Winnicott (1974) relates the first three modes of display ("implicit," "projective mimetic," and "introjective mimetic"; see also Jennings, 1990) with three steps in the development of self-awareness, which he glosses as "me," "not-me," and "not-not-me." Introjective mimetic communication includes pantomiming praxic actions, such as hitting an imaginary nail with an imaginary hammer. Pretend play likewise becomes introjective with the onset of role-play (Jennings, 1990; Winnicott, 1974). Instead of using a toy airplane to represent a real one (projective), the child can now internalize this idea, using his or her whole body as a "toy" and pretending to *be* an airplane (introjective).

Mark-making behavior, although still implicit, develops into swirling mandalas and abstract patterns (Jennings, 1990), including vertical lines that Jennings and Minde (1993) associate with the child's developing body image. Six months later, the mandalas develop into faces, and children begin to draw ideographic figures, mainly of people, especially family members (Jennings, 1990). Initially, only the "contact organs" are represented (hands, arms, eyes, mouth, etc.; Jennings & Minde, 1993). Drawing people and social scenarios appears to be continuous with role-play; it is a kind of story telling—introjective rather than projective performance. Implicit communication is also developing as children begin to express and recognize new emotions relating to self-value, such as pride, shame, guilt, and hubris (Parker et al., 1994).

Again, the buildup of new displays leads to a new level of self/other awareness—mind reading ability or "theory of mind" (ToM) (Table 4.2)—the ability to recognize epistemic mental states (e.g., thinking, imagining, guessing, and believing) in one's own mind and the minds of others (Baron-Cohen, 1995). The onset of explicit ToM (i.e., reflectively conscious ToM) is usually thought to occur at approximately age 4 years, although Judith Dunn (1991) found that children playing "in the wild"—as opposed to the unfamiliar conditions of the psychology lab—show such ability 6 months earlier. True surprise—which depends on awareness of false expectations—cannot be expressed or understood before this age (Happé & Frith, 1996). Autistic children, lacking ToM, often mistake the surprised face for one of fear.

Four-year-old children, who possess explicit ToM, can be hypnotized for the first time (Bliss, 1986). Hypnosis—mind influencing mind—presumably depends on reflective awareness of minds. A year or two later, children are ready to play games with formal rules in which there are winners and losers (Parker & Milbraith, 1994). At approximately the same time, dressing-up behavior begins along with more complex role-play and scripted theater-like performances (Parker & Milbraith, 1994). Displays are becoming increasingly conventionalized.

Hypnotic ability peaks at approximately age 7 years, and at this age role-play can become so intense that lonely children can create "imaginary playmates" with independent (dissociated) personalities (Bliss, 1986). I infer that "theater of mind"—the ability to imagine social scenarios with toy people who behave as though they have minds of their own—must be established by this time (Whitehead, 2001).

Language has not been mentioned so far because this seems to follow a precocious schedule suggesting some hard-wired basis. Babies within the womb are already tuning in to the sounds of their native tongue (Moon, Lagercrantz, & Kuhl, 2012; Partanen, Kujala, Näätänen, Liitola, Sambeth, & Huotilainen, 2014); phonemic competence is established at approximately 6 months (Eimas, 1985); and the first words are uttered at 12 months (Trevarthen, 1995)—coinciding with the onset of projective mimesis. Personal pronouns are understood at 20 months (Lewis, 1994); the verbal explosion occurs at approximately 24 months, and language rules are fully understood by 30 months (Miller & Gildea, 1987; Templin, 1957).

Conventional communication includes much more than just language (Burling, 1993; Whitehead, 2001). It includes conventional gestures both polite and rude, language-like signals such as nodding the head to say "Yes" and sounds of the "hm" and "uh-huh" variety, mathematical denotations, musical scores, and traffic signs. We continually invent new ones as the need arises.

It takes the whole of childhood to achieve the idealism and principled morality that typify adolescence (Parker et al., 1994), and perhaps even longer to develop economico-moral personae—the conventional roles we assume in adult life (Whitehead, 2003).

The developmental sequence from birth to adulthood is shown in Table 4.2.

Conventional displays, especially conventionalized role-play, are virtually constitutive of human culture—most obviously so in ritual, wealth display, and the cultural arts. However, as Mead (1934/1974), Goffman (1959), and Turner (1982) made clear, the whole of everyday life resembles a costume drama. We all wear clothes that say something about who we are, what we are doing, or how we want to be perceived by others. In every known human society, people alter the appearance or sensory properties of their bodies—with clothes, coiffure, cosmetics, soap, perfume, jewelry, tattooing, scarification, or frank mutilation. Even in the heat of the Kalahari Desert, Bushmen wear leather

**Table 4.2. The Spiral Relationship Between Social Awareness and Social Displays From Birth to Adulthood**

| | | | | | |
|---|---|---|---|---|---|
| *Primary intersubjectivity* | Implicit communication | ⟶ | Implicit play | ⟶ | Implicit performance |
| *Secondary intersubjectivity* | Projective mimetic communication | ⟶ | Projective mimetic play | ⟶ | Projective mimetic performance |
| *Self as value* | Introjective mimetic communication | ⟶ | Introjective mimetic play | ⟶ | Introjective mimetic performance |
| *Theory of mind* | Conventional communication | ⟶ | Conventional play | ⟶ | Conventional performance |
| *Economico-moral personae* | | | | | |

aprons to conceal their genitals and—perhaps by association of sex with pollution—the anus. Sexual modesty appears to be a cultural universal, and it commonly involves concealment of the genitals. No chimpanzee alpha male would consider this a good idea. We are the only apes that systematically alter the appearance of our bodies, and in such culturally diverse ways. Among our innate display abilities, role-play—pretending to be something we are not—is the most fundamentally essential to human culture. In effect, we spend much of our adult lives pretending we are not apes. Human culture involves wholly-believed-in role-play (Whitehead, 2003), which just happens to be a widely accepted definition of hypnotic trance (Heap, 1996). Hypnosis researcher Charles Tart (2009) refers to the encculturated state as "the consensual trance," a concept that he uses to critique "the dogma of materialism" in Western science. Many centuries ago, Asian mystical writers observed that the Self we believe ourselves to be is a delusion, along with our perceptions of reality.

In summary, we have three kinds of display in four modes, with displays in one mode scaffolding the emergence of the next level of self/other-awareness, along with displays in a higher mode. This looks like a matter of "design engineering." That is, you have to do a specific kind of action to achieve a specific result. The human mind and brain may develop in the way they do because there is no other way of doing it. If so, similar steps in a similar sequence must have been taken during human evolution.

I do not have space here to discuss the archeological and fossil record in detail, but elsewhere I have shown that the record is consistent with such a sequence (Whitehead, 2003, 2008a, 2010c)—although archaeological evidence accumulates rapidly, and future findings may or may not support my thesis. However, I will briefly discuss brain expansion. Figure 4.4 shows cranial capacities of fossil hominins across the past 3.5 million years (De Miguel & Henneberg, 2001). It suggests two major periods of accelerated brain expansion (although De Miguel and Henneberg argue that no "Rubicons" can be inferred from cranial capacity data alone, there were also changes in brain structure and behavior across these transitions; Whitehead, 2003, 2010c). According to the play and display hypothesis, the first phase was triggered by the emergence of song-and-dance display and the second by a major

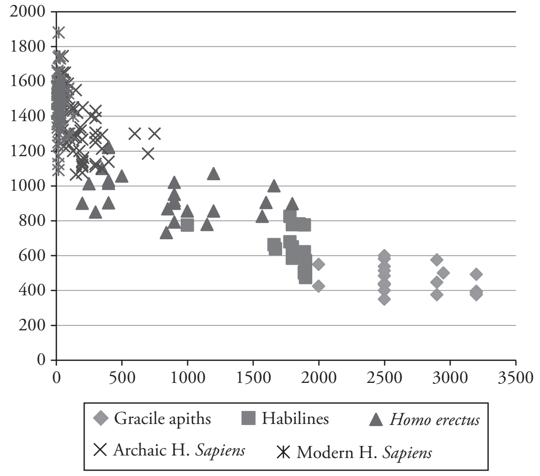

**Figure 4.4** Hominin cranial capacities from 3.5 million to 10,000 years ago.

Source: Data from De Miguel and Henneberg (2001).

elaboration of pretend play abilities (Whitehead, 2003). This second phase may in fact comprise two distinct phases (Watts, 2014)—in the first, both bodies and brains got bigger, and in the second, brain expansion accelerated while bodies actually got smaller. It is tempting to speculate that these later phases were associated with projective and introjective mimesis, respectively. If so, then we have three phases of brain expansion, associated with the emergence of secondary intersubjectivity, self-value, and mentalizing ability, as in Table 4.2.

Brain expansion ceased approximately 200,000 years ago, with brain structure not discernibly different from what we find in people living today (Power, 2014; Watts, 2014). We may infer that a fully modern culture-ready brain had evolved by this time. This final transition is marked by the first evidence of ritual pantomime (Watts, 1998; 2009, p. 74; 2010, p. 393; 2014), which implicates the beginning of modern culture and completes the four-step evolutionary sequence suggested by child development (Table 4.2).

According to the play and display hypothesis, the advent of modern culture would explain the cessation of brain expansion because social cohesion maintained "from the outside" by constitutive rules and formal institutions would not require such finely controlled displays. Following the agricultural revolution, brains actually got smaller. This could be explained as a consequence of malnutrition (Cohen & Armelagos, 1984; Cohen & Crane-Kramer, 2007; Larsen, 2002; Mummert, Esche, Robinson, & Armelagos, 2011; cf. Gage & DeWitte, 2009)—causing both bodies and brains to get smaller. However, as nutrition improved, bodies got bigger again, but brains did not. Furthermore, the bodies of foragers also got smaller as they were displaced by farming populations and adapted to life in the most improvident regions of the earth. Foraging people tend to be relatively small-bodied to this day—yet their brain-to-body mass ratios are generally higher than those of post-agricultural populations (Beals, Smith, & Dodd, 1984). It would seem that foragers were less affected by brain size reduction than agricultural peoples, as might be expected in the presence of top-down social controls exerted by an aristocratic hierarchy (cf. Hayden, 1992).

## The Culture-Ready Brain

Collaborations between neuroscientists and sociocultural scientists have led to a rapid expansion of our understanding of the social brain and the effects of culture on the brain. However, to understand the culture-ready brain—the functional anatomy that makes it possible to create, maintain, and evolve human cultures—requires a mapping of the neural correlates of social displays, and this is still a relatively neglected area.

The discovery of mirror neurons might have led to a renewed interest in social mirror theory but, instead, the Parma team responsible plumped for Paul Harris's (1991) simulation theory (Gallese & Goldman, 1998) that, in effect, treats human infants as excellent mimics as opposed to spontaneous individuals who are proactive in their own socialization and enculturation. Furthermore, the fortuitous fact that mirror neurons were first discovered in monkey grasping cortex led to a spate of neuroimaging studies of grasping, hand–object manipulation, and tool use in humans (Grèzes & Decety, 2001). Three studies used silent videos of dance as an interesting alternative to manual action in the study of the motor mirror system (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Cross, Hamilton, & Grafton, 2006), but only one sought to map the neural correlates of dance per se (Brown, Martinez, & Parsons, 2006). There have been three imaging studies of projective pretense (German, Niehaus, Roarty, Giesbrecht, & Miller, 2004; Smith, Englander, Lillard, & Morris, 2013; Whitehead, Marchant, Craik, & Frith, 2009), but only one (Whitehead et al., 2009) specifically investigated pretense as a form of play. In addition, there has been one study of role-play (Whitehead, 2003) and a few studies of mirror networks involved in the perception of facial expressions and emotion (Avenanti, Bueti, Galati, & Aglioti, 2005; Gallese, 2001; Singer & Frith, 2005; Singer, Seymour, O'Doherty, Kaube, Dolan, & Frith, 2004; for review, see Rizzolatti, Fogassi, & Gallese, 2006).

Only three forms of social display have been extensively researched by neuroscientists: language, music, and narrative. These exceptions may reflect a perception of such displays as related forms of "communication, "and thus relevant to cognition and information processing, whereas music and narrative, although they necessarily involve communication, are forms of performance (Whitehead, 2001). Performance, commonly characterized by repetition and redundancy, concerns communal experience and communal action—not communication. You can repeatedly enjoy a favorite piece of music or a good story, long after it has ceased to communicate anything new by way of "information."

One reason for this research bias, I believe, is the current emphasis on cognition rather than performance, with an assumed input → processing → output model derived from computing. However, the brain is a doing organ before it is a thinking organ, which means that output must come first. This is true both phylogenetically and ontogenetically. Clearly, animals must be able to move (output) before neurons (processing) can evolve, and without such linkage to muscle cells, sense organs (input) would serve no function. Similarly, it has been shown that during fetal development, brains send out efferent fibers to muscles (output) before they receive afferents from sense organs (input) (Trevarthen, 1985). Likewise, social displays are output-first behaviors. As Trevarthen has shown, the input → processing → output model of cognition is wholly inadequate to capture the spontaneous creativity of human infants (cf. Shore, 1997). He comments, "Cognitive science, restricting the roles of motivation and emotion, puts childhood play and imagination behind bars" (C. Trevarthen, personal communication, November 22, 2009).

Nevertheless, what is known about the neural correlates of social displays is at least suggestive, and it is consistent with the play and display hypothesis (for more complete details, see Whitehead, 2010c, 2012; Whitehead et al., 2009).

### *The Motor Mirror System*

Figure 4.5 shows the presumed mirror system for body movement in the right hemisphere of the brain. Two main areas are involved—the prefrontal operculum and the superior parietal lobule (Grèzes & Decety, 2001). The prefrontal operculum in the left hemisphere includes Broca's area, classically associated with motor sequencing for speech. The opercular areas in both hemispheres, however, are involved in body movements more generally (Buccino et al., 2001). The superior parietal cortex is part of the dorsal visual stream and has a navigational function, mapping space in body-centered coordinates. The various parts of the body map onto these mirroring areas in a somatotopic manner, like a classical motor homunculus (Buccino et al., 2001). Praxic gestures activate this system mainly in the left hemisphere, whereas expressive gestures recruit more bilateral activity (Grèzes & Decety, 2001). Inside the lateral fissure—adjacent and dorsal to the opercular area—is the anterior insula, associated with mirror responses to emotion (Avenanti et al., 2005; Gallese, 2001; Singer & Frith, 2005; Singer et al., 2004; for review, see Rizzolatti et al., 2006).

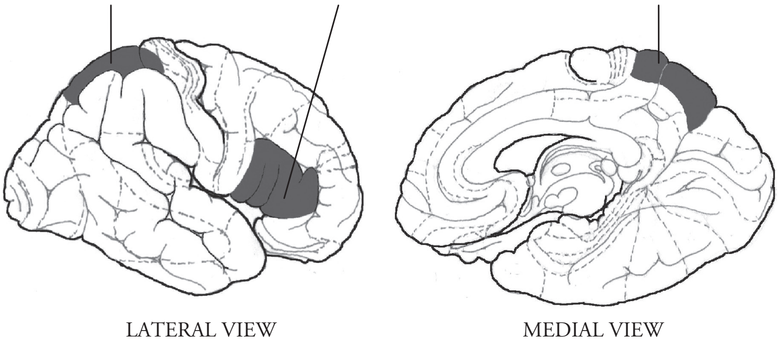

**Figure 4.5** Motor mirror system.

### *Dance*

Dance, as would be expected, also activates the motor mirroring system, with the addition of three parietal areas—inferior parietal lobule, posterior cingulate gyrus, and precuneus—and two temporal areas—temporal pole and primary auditory cortex (Figure 4.6) (Brown et al., 2006; Calvo-Merino et al., 2005, 2006; Cross et al., 2006). It seems curious that auditory cortex is activated even when watching silent videos of dance—perhaps a consequence of imagined music. It may also be noteworthy that this area is the only primary sensory cortex that is much expanded in human relative to chimp brains (Deacon, 1992). Parts of the inferior parietal lobule and the temporal pole have been regularly implicated in theory of mind tasks (Frith & Frith, 2003)—that is, reflective consciousness and assessing mental states in others.

According to the play and display hypothesis, song and dance display was established by the time the first *Homo* species emerged (Whitehead, 2003), and a prominent inferior parietal lobule is apparent for the first time in fossil crania of these early hominins (Tobias, 1987). This much-enlarged structure is strategically placed for multimodal integration, bordered on all sides by visual, auditory, somatosensory, and motor cortices. Coordination of all these modes is clearly crucial for communal dance. The temporal pole is another multimodal integration area. Of particular relevance to dance may be its postulated role in the integration of complex perceptual inputs with emotional responses (Olson, Plotzker, & Ezzyat, 2007).

The precuneus appears to be a recently expanded structure that lies adjacent to the superior parietal motor mirroring area. Its functions are currently believed to include mental imagery relating to self perceptions, together with visuospatial and motor imagery. It has also been hypothesized to be a "central hub" of consciousness, being one of the areas that is most deactivated during slow wave and REM sleep as well as coma and vegetative states, and most active during wakefulness, attentional states, and introspective daydreaming (theater of mind) (Cavanna & Trimble, 2006).

### *Projective Pretend Play*

Of three functional imaging studies observing projective pretense (German et al., 2004; Smith et al., 2013; Whitehead et al., 2009), only one specifically investigated pretense as *play*—using videos in which the actor signaled playfulness by facial expression and body language (Whitehead et al., 2009). In this study, and in one study of mimed instrumental actions (German et al., 2004), activity was seen in four areas common to dance and also the parietotemporal border, superior temporal sulcus, and medial/orbital prefrontal areas (Figure 4.7). Whereas dance activated two areas commonly associated with ToM, these studies implicated a comprehensive set of presumed ToM areas. German et al. inferred that observing pretense automatically invokes mentalizing activity. Social mirror theory, however, suggests that pretend play is necessary for the development of ToM, and that ToM subsequently engages areas originally dedicated to pretend play. The question is complicated by the fact that behavioral studies implicate implicit ToM abilities in infants as young as 15, 13, and even 7 months (Kovács, Téglás, & Endress, 2010; Onishi & Baillargeon, 2005; Onishi, Baillargeon, & Leslie, 2007; Surian, Caldi, & Sperber, 2007). Smith et al. suggest several reasons why their study did not show ToM-like activity. Most authors agree that there is a relationship between ToM and pretense, but current evidence is not sufficient to clarify the nature of that relationship.

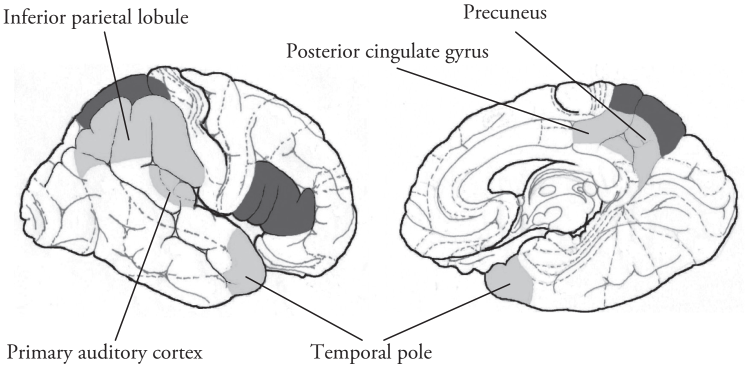

**Figure 4.6** Main cortical areas associated with dance.

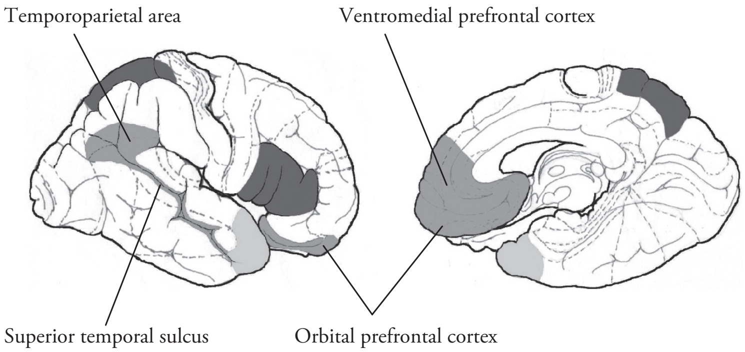

**Figure 4.7** Main cortical areas associated with projective pretense.

What is not in question is the social importance of the areas shown in Figure 4.7. The classic case of Phineas Gage, who suffered a massive lesion of his ventromedial and orbital prefrontal cortices (Damasio, 1994; Dolan, 1999; Harlow, 1848), and similar subsequent cases (Bechara, Damasio, Damasio, & Anderson, 1994; Damasio, Tranel, & Damasio, 1990; Damasio & Van Hoesen, 1983) indicate that these brain regions are not required for general intellectual functioning but are vital to empathy, social bonding, social insight, moral concern, and social responsibility. Two individuals who sustained such injuries in the first 15 months of life, in addition to the expected impairments, also failed to learn social rules and conventions (Anderson, Bechara, Damasio, Tranel, & Damasio, 1999). Hence, these regions seem to be essential for the development of economico-moral persona.

As the play and display hypothesis would lead one to expect, the relatively massive enlargement of the prefrontal lobes occurred during the later phases of hominin brain expansion (Bruner & Holloway, 2010), and prefrontal lobes are among the last to mature in late or post-adolescent development (Giedd et al., 1999; Huttenlocher & Dabholkar, 1997; Perrin et al., 2008).

## *Introjective Pretend Play*

There has only been one study of role-play (Whitehead, 2003; Whitehead et al., 2009). However, many authors assume continuity between role-play and narrative (Mar, 2004; Whitehead et al., 2009). When we listen to a story, read a novel, or watch a play or movie, we identify with the characters involved—so closely that we may care about what happens to them almost as though it were happening to ourselves. That is, we are mentally role-playing these characters, and with a willing suspension of disbelief. This is introjective make-believe (Whitehead, 2001).

Figure 4.8 shows the collective results from the role-play study (Whitehead, 2003) and narrative studies reviewed by Mar (2004). This shows that introjective pretense involves all the areas mentioned previously with the addition of dorsolateral prefrontal cortex. This set of brain areas includes the “default system” of the brain—areas that, in imaging studies, are more active during supposed periods of “rest” than when participants are engaged in cognitive tasks. It is likely that these areas are involved in daydreaming (D’Argembeau et al., 2005; Iacoboni et al., 2004; Kennedy, Redcay, &

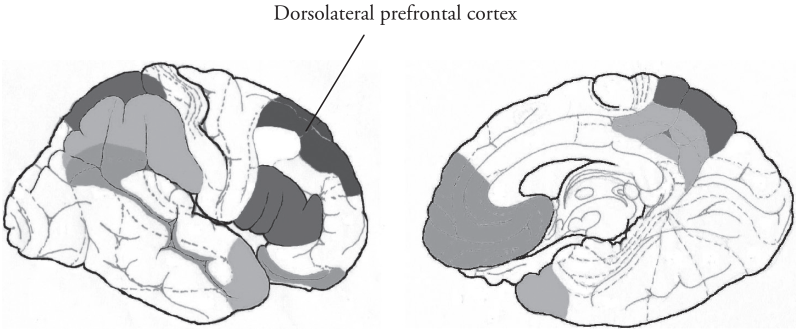

**Figure 4.8** Main cortical areas associated with introjective pretense.

Courchesne, 2006; Mar, 2004). Many authors assume further continuity between role-play, narrative, and daydreaming (telling yourself stories or “theater of mind”) (Mar, 2004; Whitehead, 2001, 2003; Whitehead et al., 2009).

### *Conclusion*

It has not been shown that all the areas implicated in Figures 4.5–4.8 include mirror neurons, although one would expect that social displays require mirror systems—as has been shown for facial expressions (Avenanti et al., 2005; Singer & Frith, 2005; Singer et al., 2004; for review, see Rizzolatti et al., 2006). Michael Arbib (2002) suggested that brain expansion during human evolution was characterized by proliferation of mirror networks, with newer networks subsequently adapting to new functions. Certainly, the imaging evidence reviewed previously (although more—and more appropriate—studies are needed) suggests a progressive evolution of displays, with more recent displays built on and extending beyond older ones. Furthermore, the implicated sequence (dance, then projective pretense, and then introjective pretense) accords with the play and display hypothesis. It is also worth noting that introjective pretense involves several areas common to language—even though the narrative studies (those that used words rather than pictures to tell a story) included controls that subtracted language activity from the resulting brain activation maps. This suggests that language, too, depended on an earlier display system (role-play). One would not expect that language could emerge in the absence of sophisticated mimetic abilities, and of course ritual/speech coevolution theory specifies ritual pantomime—or role-play—as the essential precursor of language.

In total, there may be six or more overlapping mirror systems in the brain, involved in body movements, affective displays, song-and-dance display, projective mimesis, introjective mimesis, and language (Whitehead, 2010c).

## Final Remarks

Bronwen Cohen, Chief Executive of Children in Scotland, introducing an international conference organized by that body (“Making Space,” October 7–8, 2010), stated, “We, at Children in Scotland, do not accept the cynical view that politicians will not listen to independent advice, expert opinion, and research-based evidence.” I took this to heart because I was one of the cynical ones, and I think I can be excused for holding such a view. Only the previous year, Vernon Coaker, the UK schools minister, rejected the *Cambridge Primary Review*—the largest independent review of English primary education in 40 years—as “a retrograde step” and “completely counterproductive,” despite the fact that leading voices in education appealed to the government to face up to the devastating criticisms in the report and to move on its recommendations. Every teaching union gave the report its backing, and head teachers’ leaders said any attempt to ignore it would be an “act of weakness” on the government’s part (*The Guardian*, Friday October 16, 2009). One fundamental—and evidently prophetic—criticism the review made was that ministers refuse to take independent expert advice in formulating schools policy. The review claimed that, since 1997, the government has intervened in the way schools teach on an unprecedented level, imposing a “state theory of learning” with “Stalinist overtones” (Alexander et al., 2009).

The aim of this chapter has been to contribute to current understandings of child development and to add evidential substance deriving from performative psychology, sociology, linguistics, ethnography, ethology, paleoanthropology, and neuroscience to support the policy recommendations of, for example, the Alliance for Childhood in the United States and the *Cambridge Primary Re*view in the United Kingdom—whose views are already well supported by empirical research on educational practices and the effects of social disparities. This may sound a little ethnocentric, but the rest of Europe, Asia, and nations elsewhere for the most part do not impose formal education before the age of (UNESCO Institute for Statistics). Developing nations in particular have other problems, such as ensuring that all children have access to education or that girls and boys have equal educational provision—problems that, in my view, merit more aid than currently donated by developed nations. In pursuing my aim, I hope the optimism shown by Children in Scotland prevails, and that policymakers do in fact realize that the best ideas do not always come from civil servants.

The evidence I have mentioned concerning the two major phases of arborization and pruning seems to lend tentative support to the widely accepted view that formal education should not begin before the age of 6 years. But my main take-home message concerns the vast importance of play and performance. I have argued that uniquely human social displays are the reason for our large brains, essential to healthy child development, fundamentally constitutive of human culture, and indispensible to the healthy functioning of human societies. If we want to ensure that our children grow up—as they are naturally inclined to do—into happy, healthy, and productive members of society, we must defend and develop our children's access to play and artistic expression. Mental health, social well-being, and economic prosperity can best be ensured if policymakers support and facilitate, but do not interfere with, childhood play and spontaneous self-expression.

One anonymous reviewer suggested I should say more about how we support and facilitate spontaneous output-first behaviors in children. Much good work is going on in this regard, but I have space here only for a couple of—it is hoped—useful pointers.

First, I note that the *Cambridge Primary Review* recommends more outdoor lessons after the Scandinavian model because of the proven benefits to children, including improved academic achievement. At Hval Gaard Kindergarten inNorway, for example, 4- and 5-year-old kindergarten children are outdoors all the time, regardless of weather conditions (Forstad, 2005). Norwegians have a saying: "There's no such thing as bad weather, only bad clothing" (Forstad, 2005). Richard Louv (2005/2008), in a book that launched the "No Child Left Inside" movement in the United States, comments:

> Nature Deficit Disorder describes the human costs of alienation from nature, among them: diminished use of the senses, attention difficulties, and higher rates of physical and emotional illnesses. (p. 34).

Of course, urban schools cannot always conduct forest play along Norwegian lines, but municipal authorities can usually be persuaded to make park spaces available for school use, and in the light of current research, there is now no excuse to deny outdoor recess to schoolchildren, especially among underprivileged communities. A randomized controlled trial of a popular recess program in low-income US schools (Robert Wood Johnson Foundation, 2012–2013) showed widespread benefits, including less bullying, enhanced feelings of safety at school, increased vigorous physical activity during recess, greater readiness to learn, and more time for classroom teaching.

Second, I note some current views from Finland, which also take account of phases of brain development. Bergstrom and Ikonen (2005) observe that the expression "fantasy world" is often used as a pejorative, and they suggest "possibility world" as a more positive alternative. Fantasy explores possibilities and so is a psychological parallel to science; indeed, scientists who propose seminal ideas and make important discoveries undoubtedly use fantasy as part of their toolkit. Bergstrom and Ikonen conclude that order and structure imposed by adults is deleterious to childhood play and spontaneous self-expression:

> Children require freedom and space. Too much order can inhibit their learning. In our view, nature can provide the best environment for a child's play. This is understandable because nature is in many ways chaotic and full of "realised" possibilities. . . . When we observe children's behaviour in this natural environment we can see them observing every small detail and absorbing everything around them. In nature they find a reflection of their own "possibility" world. Nature, or outside kindergartens . . . such as exist in Finland and other Nordic countries are good examples of space that offers the freedom and possibilities for free play that young brains require. (p. 13).

Where built space is concerned, they recommend the school designs of Finnish architect Pihla Meskanen—Director at Arkki School of Architecture for Children and Youth, and Chair of Playce—who creates environments in which children can express their "possibility world" by creating their own light and shade. Finally, they conclude:

> Of course, we also need order and structure. But spaces that have four straight walls like the classrooms in many of our schools are not what is required. Why do children seek out the untidy or incomplete, ruined buildings or building sites? Buildings which offer young children the chance for them to re-order, complete or knock them down like sandcastles on the beach, provide their brains with room to grow and mature. Architects as well as brain scientists need to know about the brain. (p. 13).

I might add that educators and policymakers also need to know about the brain.

These American and Scandinavian views could have come straight from Victor Turner because they conform precisely to his theory of anti-structure. Turner referred to the "possibility world" as the subjunctive "what if?" of play, ritual, recreation, entertainment, and the cultural arts (Turner, 1982). These are all anti-structural behaviors with transformative and restorative functions.

I conclude that we need to free ourselves from negative thinking rooted in political anxieties and ideological biases—the emphasis on competition, league tables, SATS testing, and "progressive" policies—and invest more effort in protecting what we have always had: the innate playfulness that is essential to the well-being of children and the development of balanced, healthy, and socially constructive citizens.

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CHAPTER

5

# Culture as a Response to Uncertainty: Foundations of Computational Cultural Neuroscience

George I. Christopoulos *and* Phillipe N. Tobler

## Abstract

Cultures are dynamic by nature. This characteristic stems from constant changes of the natural and social environment, pressure and influences from other cultures, and evolutionary needs for adaptive responses, both at the individual and collective level. In decision and social neuroscience, individual adaptive responses to changing, unknown, or uncertain environments have been successfully described by the integration of the computational framework of reinforcement learning models with principles of game theory and microeconomics. This framework identifies a valuation system that constantly updates values attached to actions and stimuli in order to reduce reducible uncertainty and efficiently guide actions in the face of irreducible uncertainty. We propose that this theoretical and methodological framework can be fruitful in explaining dynamic cultural phenomena—an approach we term computational culture neuroscience.

**Key Words:** computational cultural neuroscience, game theory, reinforcement learning, dynamic, uncertainty, enculturation, cultural mixing, niche construction, modeling

> *Social systems can exist only because human behaviour is not random, but to some extent predictable.*
>
> —*Hofstede (1981, p. 15)*

## Culture as a Response to Uncertainty

It is not a coincidence that the previous quote by Hofstede is the very first statement of one of the seminal papers in culture research. In fact, it could be argued that any system that involves interacting agents necessitates that each of these agents can predict, with more or less uncertainty, the behavior of other agents. These elements of knowledge, shared meanings, and expectations can facilitate and speed up the exchanges of people who need to frequently interact, share resources, and swap tangible and intangible assets.

When acculturated subjects interact with other agents, predictability allows them to employ some form of expectations, most likely based on previous experiences. Imagine, for instance, somebody visiting a (probably Asian) country where bowing is a form of introduction (Figure 5.1). Our visitor already knows that she needs to bow when meeting an important stranger but might be unsure to what degree she should bow and under what circumstances. She nevertheless has some expectations (Figure 5.1A). After living in the country and via different learning mechanisms (explained later), she updates her estimation of the correct (i.e., expected) way of bowing. This is a constant process.

Instances of reducing uncertainty based on social and cultural information abound and could range from everyday behaviors, such as what to wear or what and where to eat, to more complex or comprehensive tasks, such as how to allocate time, how to engage with the other gender, how to express ideas, and how to conduct business. In all these examples,

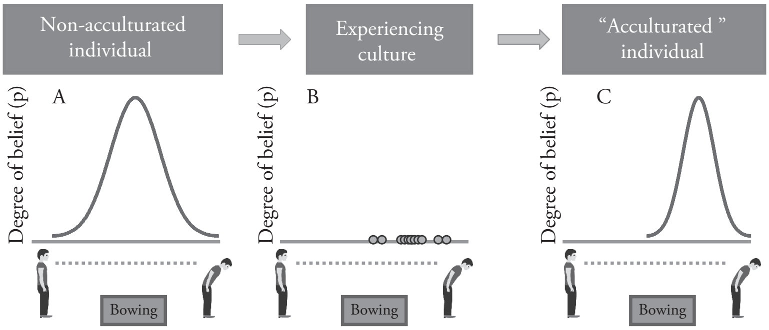

**Figure 5.1** Learning norms and expectations. (A) Each individual has some expectations about the results of her behavior and what is expected from her within a culture/society. These beliefs are rarely definite but, instead, have stochastic properties. For instance, somebody visiting an Asian country might already know that she needs to bow, but she is unsure to what degree. (B) After living within a specific culture, the individual learns via different ways (described in the main text) what are the expected behaviors (red dots). (C) Experience helps the individual to reduce uncertainty about what is expected. This process is continuous and dynamic and can apply to many domains, such as trust, reciprocity, and even clothing. (Note that the images and distributions used here are for illustration only and thus do not represent how exactly the updating will impact the shape of the distribution.)

agents usually will modify and follow a set of expectations, norms, and rules in order to guide their judgments and behavior.

These learned and shared "networks of knowledge" (Hong, 2009) are a critical (but not the only) aspect of culture. Yet, what is usually assumed but often not spelled out is that (1) they are *uncertain* (i.e., probabilistic), (2) they are *dynamic* and adaptive rather than static, and (3) they are *learned*. The first characteristic ('uncertainty') stems from two sources. First, not everyone is or behaves the same, and therefore even if an average response is expected, there are always deviations from that response and such deviations are expected as well. This means that the culturally expected behaviors and meanings could be represented (and internalized) as a probability distribution. Second, uncertainty also arises from internal variability, noise, and fluctuation structurally inherent in brain biology and cognitive function. This has long been recognized as a major determinant of the function, inferential processes, biases, and illusions for many systems, neural and cognitive (Beck, Ma, Pitkow, Latham, & Pouget, 2012; Li, Lindenberger, & Sikstrom, 2001; Nagengast, Braun, & Wolpert, 2011; Servan-Schreiber, Printz, & Cohen, 1990). The second characteristic ('dynamic') stems from the fact that the environment within which each culture functions is constantly changing. The change could be due to external factors (other cultures, migration and cultural mixing, nature and quantity of resources available, climate variations, etc.) or factors that are produced by the culture itself (technology, demographic characteristics, etc.).

The first two characteristics (uncertainty and dynamic character) directly imply the third: Culture has to be (constantly) learned. Thus, probability distributions and their representations change over time. Learning about the environment is the critical tool that successful agents use to reduce uncertainty as much as possible. It is therefore obvious that in order to understand the rules that explain the formation of cultures and the interaction of agents with cultures, we need to incorporate the mechanisms of learning as one of the basic cognitive abilities that underlie cultural behavior.

Opportunity and need for cultural learning may be particularly obvious in specific circumstances, such as the following:

- Development and aging across the lifespan: How and when do children learn these "networks of knowledge"? How do adaptive responses change as a function of age—for instance, during adulthood and old age?
- Biculturalism and cultural interactions/mixing: When humans move from one culture to another, how do they learn and update their expectations and rules? How can such learning be facilitated or inhibited?
- Adaptive responses to increased uncertainty or change: In times of major transitions (e.g., during a technological change), how do cultural agents respond to new information and challenges?
- Niche construction: How do cultural agents find their place within culture, and how do their actions interact with culture? This can be achieved by a combination of socialization (including

observational learning), exploration, and individual learning.

All these processes are aspects of socialization and enculturation. Socialization and enculturation are interrelated concepts characterizing the interaction of an individual or a group with societal and cultural norms. Both concepts are (1) complex and multifaceted, (2) inherently dynamic, and (3) based on members of a society (e.g., family, friends, institutions) *reinforcing* behaviors of newcomers (including children) (Rossano, 2012; Snyder, Schrepferman, & St. Peter, 1997). We therefore believe that the framework presented here could help in elucidating some of the mechanisms underlying these central processes.

The primary aim of this chapter is to suggest a possible basic mechanism for understanding the dynamic aspects of agent–culture interactions in the form of a computational framework (for a framework describing the integration of culture research and cognitive science, see Christopoulos & Hong, 2013). To this effect, we introduce the formal tools, theories, and models of individual learning (and specifically reinforcement learning (RL)) and decision-making under risk in the study of dynamic cultural phenomena. These tools may be particularly useful for describing individual responses to culture as well as actions influencing culture. To the extent that they improve our understanding of psychiatric conditions, they could also help us reveal differences in the expression of psychiatric diseases across different cultures (Collins, Insel, Chockalingam, Daar, & Maddox, 2013).

The chapter is organized as follows. The next section explains the general tenets of RL; subsequently, we present basic computational and neuroscientific approaches underlying RL. Next, we discuss how RL has been used to examine socially mediated learning—that is, learning from others when the outcomes of the agent are independent of others (observational learning) and learning when the outcomes of the agent depend on what others do (game theoretic approaches). Then, we summarize RL predictions of behavioral and neurocomputational responses to uncertain and volatile environments. We conclude by offering a list of predictions/working hypotheses that arise directly or indirectly from this framework.

## Reinforcement Learning: Principles and Their Applications in Culture Research

Imagine two people moving after they have lived their lives until now in one place. Person A moves from a jungle in New Guinea to New York, whereas person B (our visitor mentioned previously) moves from New York to Beijing. Person A will presumably have a stronger culture shock than person B, who has previous experience with urban lifestyle. However, both will face considerable uncertainty about how to behave in the novel culture. What was appropriate behavior before, may now no longer be appropriate. One way of dealing with this uncertainty for our two movers is to either learn new or modify existing behavior and knowledge. Learning may occur from scratch and on-the-go through trial and error, through similarity-dependent generalization from knowledge already acquired in the movers' own culture, or by testing models or hypotheses developed before or after moving. Generalization—that is, extending rules and behavior from previously learned to similar conditions (Kahnt, Park, Burke, & Tobler, 2012)—may be more successful for person B than for person A, who may be better off learning from scratch. Both may benefit from basing their learning on knowledge about how the other culture works. Specifically, this may be knowledge about contexts, actions, expectations, and rules in the new culture ("culture-specific actions, states, and state transitions"). Such knowledge corresponds to a model of the culture and can be acquired through a specific form of learning called "model-based learning" (discussed later).

In the following, we introduce basic learning terminology and phenomena as applied to cultural contexts, discuss the distinction of model-free and model-based learning, and suggest how learning can reduce uncertainty. We focus on (a limited part of) value-based association learning primarily because of space constraints (for further detail, see Pearce, 2008). However, it should be kept in mind that there are many other forms of learning, such as conceptual learning, statistical learning, imprinting, habituation, and sensitization. Given that formal rules have been developed for describing individual associative learning, the possibility arises that these rules may provide useful building blocks for a computational approach to culture science. We also briefly discuss neuroscientific evidence suggesting that the formal terms employed by these learning rules can be used to accurately describe neural activity during learning. This, in turn, may suggest that the neural mechanisms underpinning individual learning may play a role also during learning about culturally relevant outcomes.

### *Basic Phenomena and Terminology: Acquisition, Extinction, and Reversal*

When moving from New Guinea to New York, person A will face many novel situations. Some of these situations have consequences irrespective of what she does, whereas with other situations, the consequences depend on her showing a particular behavior. For example, many of the novel and loud traffic noises of the big city occur and (may) elicit fear no matter what (i.e., independent of the actions of person A), but the sound of a car horn may occur and elicit fear only if person A behaves in a particular way (crossing the street). This distinction leads to a common classification of associative learning phenomena: classical (or Pavlovian) versus instrumental (or operant) conditioning. Roughly speaking, classical conditioning corresponds to stimulus-outcome learning, whereas instrumental conditioning corresponds to action-outcome learning, although instrumental conditioning can also be under the control of stimuli (discussed later). Indeed, the two forms of learning often occur in parallel and can be difficult to separate.

In the wake of the cognitive revolution and based on empirical data, associative learning research no longer followed the behaviorists in assuming that it is stimuli that are associated with each other but representations of these stimuli (Dickinson, 1981). In the following, we presuppose this but sometimes use the stimuli as shorthand for their representations. In classical conditioning, unconditioned stimuli, such as food or electric shock, are paired with neutral stimuli. Unconditioned stimuli are called "unconditioned" because they elicit behaviour, such as salivation or freezing, on their own and tend to be related to basic needs, such as hunger or safety. By contrast, conditioned stimuli typically elicit little or no behavior on their own and tend to be unrelated to basic needs. By repeated presentation of the unconditioned stimulus after the conditioned stimulus, the conditioned stimulus alone can elicit the behavior originally elicited by the unconditioned stimulus. In order for conditioning to occur, the conditioned stimulus typically has to provide information about the occurrence of the unconditioned stimulus, such that the probability of occurrence of the unconditioned stimulus is higher or lower when the stimulus is present than when it is absent. This transfer can be referred to as *acquisition* of a conditioned response, in the sense that the conditioned stimulus gradually comes to elicit a response, such as salivation or freezing, which it originally did not.

Some examples might be useful. The person living in a very rural area of New Guinea (person A) might have learned that seashells are valuable because they are used as the main medium of exchange. Seashells are important because they predict delivery of food. When she moves to New York, she now has to learn to associate a previously meaningless piece of paper (banknote) with food. The banknote will now become a conditioned stimulus. A more instrumental example, governed by the same principles, is described in Figure 5.2A. Following the example described in Figure 5.1, person B can learn the correct angle of bowing by incorporating social feedback (e.g., an approving smile) from the members of the culture.

Conditioned responses may not only be acquired but also be extinguished. Such *extinction* learning occurs when a fully conditioned stimulus is no longer followed by the unconditioned stimulus. Extinction could occur when persons A and B move and slowly forget the rules associated with the culture in which they previously lived. Behaviorally, this leads to the gradual reduction of conditioned responding to the conditioned stimulus. However, conditioned responses can re-emerge after the passage of time or when contexts change (Bouton, 2014). In other words, the original (excitatory) memory trace can still be expressed in behavior. Thus, **extinction is not simple unlearning** but, rather, corresponds to the formation of a new association between the conditioned stimulus and "no outcome." Note that the literature often uses the term "in extinction" to denote test situations in which conditioned stimuli are presented without unconditioned stimuli in order to measure conditioned responses without contamination by unconditioned responses. In this case, learned behavior will not have extinguished yet (but eventually would if testing were to be continued).

In our examples, extinction needs to happen when person A starts to use banknotes instead of seashells. The association of seashells with food should be weakened, at least within the specific cultural framework. In the bowing example (Figure 5.2C), extinction happens when person B, who was acculturated in a Western country and used to shaking hands or even hugging, now needs to learn that shaking hands or hugging is not an expected form of social introduction and greeting. In the new country, these behaviors will not be rewarded (or could even be socially punished or disapproved). Therefore, via the mechanisms of extinction, these behaviors will lose their value and therefore gradually be discontinued.

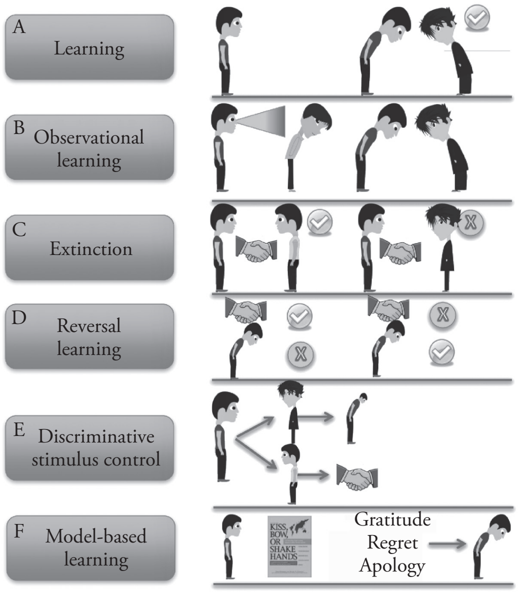

**Figure 5.2** Some ways of learning. (A) Reinforcement learning: Somebody can learn by associating actions or stimuli with rewards and punishments, including social ones such as a smile or disapproval. This type of learning tends be slow but simple and powerful. (B) Observational learning: Somebody can learn by observing how others behave. This type of learning has the advantage that it is relatively costless. (C) Extinction: If somebody moves to another culture or if there are drastic changes within the culture, then the previously rewarded behavior is no longer rewarded. By extinction, the behavior stops. (D) Reversal learning: Previously nonrewarded behaviors (e.g., bowing) are now rewarded, whereas previously rewarded behaviors are no longer rewarded (e.g., handshake). Both panels C and D require new learning. (E) Discriminative stimulus control: An individual can learn to behave depending on the situation. Therefore, depending on whom he or she meets (stimulus), a different behavior is triggered. (F) Model-based/state-based learning: An individual can learn the proper behavior by assuming a model of the world. For instance, before relocating, one could read up on the cultural norms that apply in the country to which one is moving.

Learning research is a wide field that has designed many paradigms that test for specific aspects of learning, such as the nature and richness of representations. One paradigm that has been rather popular in the behavioral neurosciences combines acquisition and extinction. This paradigm is used to study *reversal* learning. As described in more detail later, reversal learning might be critical in situations in which an agent experiences more than one culture. At any time, two stimuli are used in random alternation. Only one of them is followed by the unconditioned stimulus. After agents have learned about this, the contingencies are reversed, such that the stimulus originally followed by the unconditioned stimulus is extinguished, whereas the control stimulus is now followed by the unconditioned stimulus and to be acquired. Successful reversal requires discrimination between stimuli as well as overriding previous associations with novel ones. If agents continue to respond to the previously reinforced but now extinguished stimulus, they show *perseveration*. A not entirely serious example in the instrumental domain may be that our person B had to learn as a child not to audibly inhale air while eating noodles, but after her move this action is reinforced up to a point.

Figure 5.3D presents how reversal learning is implemented. Assume that due to some contagious disease, the health authorities in New York recommend bowing rather than shaking hands. People such as person A would therefore have to learn that shaking hands is no longer a correct form of introduction. Person A learns to stop this behavior through the absence of reinforcement (extinction). Conversely, a previously non-reinforced behavior (bowing) is now reinforced. Taking the two together results in reversal.

If person B were to move back and forth between cultures, she should learn to use discriminative stimuli to bow in one but not the other culture. If this is the case, the action is under discriminative *stimulus control*: It is produced in the presence of one but not another stimulus, and this is facilitated by dissimilar stimuli (cultures). By contrast, with *generalization*, a given action tends to be produced more frequently after more similar rather than dissimilar stimuli. Through a classical conditioning process called *autoshaping*, discriminative stimuli predicting appetitive consequences can come to elicit behavior oriented to that stimulus (e.g., keypecking), even if that behavior leads to the removal of the consequence. This illustrates the notion that classical and instrumental conditioning often occur in parallel.

With little practice, instrumental actions are sensitive to changes in the value of the consequences. When the For instance appetitive consequence of an action is no longer very likely or good due to satiation or poisoning, the associated instrumental action will be produced less frequently. As long as this holds, actions are referred to as *goal-directed*. By contrast, with much practice, responses come to be triggered automatically by stimuli, and this process is no longer sensitive to changes in value. When this holds, behavior is referred to as *habitual*. Distinct training paradigms can preferentially produce goal-directed action or habits even in the absence of variations in the amount of practice

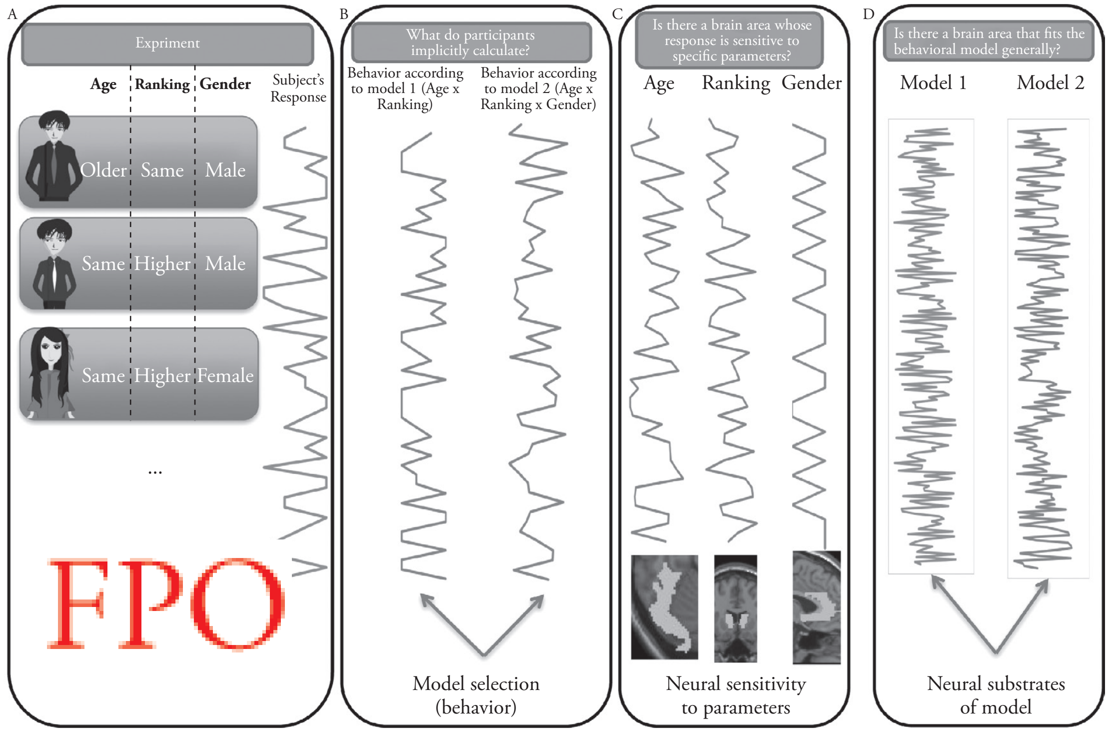

**Figure 5.3** The Computational Culture Neuroscience approach: What determines the angle of bowing? This example loosely demonstrates the advantages of computational culture neuroscience as provided through neuroimaging and formal modeling (compared to simple contrasting of conditions). Assume that somebody wanted to study how people of a specific culture decide how much they bow (dependent variable) as a function of the age, gender, and status (independent variables) of the person they meet. (A) Task: The task could parametrically vary the independent variables in many trials. A behavioral response (degree of bowing) will be needed on each trial. (B) Computational models. Different models could be fitted to observed behavior. For instance, one model will assume that what matters is a combination of age and gender, whereas another one could assume that status should be overweighed when making such a decision. The models could practically be infinite, so a careful, theory-based selection of models is useful. (C) Brain responses to specific parameters. Brain measurements can uncover otherwise hidden calculations. For instance, one can identify if different brain areas respond to age, gender, and hierarchy and also identify how they determine the behavioral response. This is a significant improvement in uncovering mechanisms because it offers a more detailed picture of the decision process. (Brain areas presented here are for illustration purposes only.) (D) Computational models in the brain: Models can comprise different components and thereby implicitly make different predictions about the neuronal responses on each trial. By fitting the expected modeled responses to the measured brain responses, one can more confidently verify the robustness of, and add biological plausibility to, the selected model. This approach can also help in identifying and explaining subtle group or individual differences. For instance, one group could update norms primarily as a function of age, whereas another group could weigh primarily status. Note that sometimes such discrepancies might not be visible from behavior alone.

(Adams, 1982). Goal-directed acting is more likely when consequences occur after every *n*th action (*variable ratio schedule*), whereas habits are more likely when consequences occur after every *n*th time period (*variable interval schedule*). The contingency between actions and consequences is weaker in the latter than in the former. Habits require less cognitive resources and control than goal-directed actions but can be maladaptive, particularly when consequences change. One example might arise when we move from a country in which people drive on one side of the road to a country in which they drive on the other side.

### *Basic Theory*

Learning theories provide simple but powerful algorithms that describe and explain how associations between stimuli, actions, and outcomes form. One class of models (Bush & Mosteller, 1951; Rescorla & Wagner, 1972) suggests that learning occurs whenever outcomes differ from predictions. This difference is referred to as surprise or *prediction error*. When a neutral stimulus is followed by reward in a simple conditioning experiment, this neutral stimulus (e.g., the green paper for person A) predicts nothing in particular. Thus, the occurrence of the reward (food) is surprising and elicits a positive prediction error. The prediction error, weighted by a learning rate parameter, is used to update the prediction for the next encounter of the stimulus. As acquisition progresses, predictions approach an asymptote while prediction errors approach zero (when the reward is fully predicted, there is no prediction error and nothing new to learn). Conversely, extinction can be captured by negative prediction errors that arise when outcomes are predicted but fail to occur (no food with seashells). Formally,

$$\Delta V_{\mathrm{A}} = \alpha\,\beta(\lambda - \Sigma V)$$

where $\Delta V_{\mathrm{A}}$ corresponds to the amount by which the value of stimulus A is updated in a trial, $\alpha$ and $\beta$ are learning rate parameters that reflect the intensity of the conditioned and unconditioned stimulus, and $\lambda - \Sigma V$ corresponds to the prediction error—that is, the difference between the value of the outcome ($\lambda$) and the value of the prediction incorporated in all stimuli present in that trial ($\Sigma V$). $\Delta V_{\mathrm{A}}$ is added to the previous value of stimulus A to determine the value predicted by A in the next trial.

The Rescorla–Wagner model describes behavior well in many learning paradigms. However, it has relatively poor temporal resolution (trial-wise; however, neural systems and even behavior are more fine-grained). Moreover, it cannot explain *second-order conditioning*: When neutral stimuli are followed by conditioned stimuli, the neutral stimuli will start to elicit the same conditioned response as the conditioned stimuli with which they have been paired even though the reward (or punishment) is not delivered. In our example, person A will learn that ATMs are valuable even though they do not deliver food. The Rescorla–Wagner rule cannot explain this because there is no within-trial learning, and if anything, prediction errors should be negative when food is not delivered. However, a real-time extension of the Rescorla–Wagner rule called the temporal difference (TD) learning rule can explain second-order conditioning.

In *TDlearning*, a trial is broken down into time-resolved states ($s_t$) that succeed each other and may or may not lead to outcomes such as reward $r_t$ (for more detail, see Sutton & Barto, 1988; Daw & Tobler, 2013). At each moment in time, individuals predict the value of reward at future time steps and update their predictions based on what happens next. However, rather than only waiting until future outcomes actually occur, they also compare their own predictions across adjacent states. Based on this, they can calculate TD errors (similar to prediction errors in the Rescorla–Wagner rule) as follows:

$$\delta_t = r_t + \gamma V(s_{t+1}) - V(s_t)$$

where $\gamma$ is a discount factor reflecting the notion that delayed reward is less valuable. The TD error at time $t$ corresponds to the difference between how valuable that state actually is (i.e., current reward (first term) plus prediction of all future reward (second term)) and how valuable the individual predicted it to be (third term). The update mechanism corresponds to the addition of the error, weighted by a learning rate, to the previous prediction, just as in the Rescorla–Wagner rule (where we called the learning rate 'intensity of the stimulus'). With the TDlearning rule, second-order conditioning finds a straightforward explanation: The occurrence of a reward-predicting conditioned stimulus elicits a positive prediction error, which in turn increases the prediction of the preceding (neutral) stimulus.

Imagine a young animal is fed the fruits of a tree by its mother. Some fruits will be larger and sweeter than others. Thus, the value of outcomes varies from sample to sample. Using TDlearning, the animal can form an expectation of how good the tree is on average. In other words, TDlearning helps the animal to form a prediction of the mean of the probability distribution of outcome values. However, the shape of a distribution of outcomes is characterized not only by the central location (mean) but also by other characteristics (moments)—for example, the dispersion (variance) and the symmetry (skewness) of outcomes. In principle, these characteristics can also be learned through prediction errors (Bossaerts, 2010). For example, for variance, the prediction error would be the difference between the predicted and the experienced variance.

Interestingly, one way of formally defining risk is through the dispersion (variance) of outcome distributions. In this view, a gamble that provides a 50/50 chance of obtaining \$10 or \$90 is riskier than a gamble that provides a 50/50 chance of obtaining \$40 or \$60. Investors typically require a higher mean to compensate for increases in variance. In other words, they are risk averse, and the value of a choice option is provided by the combination of the mean and the variance. Note, however, that other ways of capturing risk are conceivable and also the mean variance approach can be extended to incorporate higher moments such as skewness. Typically, these extended models capture choice better even if one accounts for the larger number of parameters. In any case, in order to incorporate these characteristics into choice, agents need to learn about them, and the process of adjusting predictions through the reduction of prediction errors captures such learning in a precise manner.

A variant of TDlearning, called *Qlearning*, explains instrumental conditioning. The mechanisms are the same as in TDlearning, but in addition to states, Qlearning considers also actions and bases predictions and prediction errors on state/action pairs. In our example, if person B's attempt to bow (handshake) in the new culture is followed by social (dis)approval, then it would elicit a positive (negative) prediction error. By assigning value to all the available actions, agents can choose the action with the highest value in a given state.

Note, however, that this may not always be optimal because circumstances can change and different actions could have become better. Thus, agents may occasionally want to *explore* rather than *exploit*. The question then arises ofhow the non-best action should be determined for exploration. Selecting among non-best actions uniformly and randomly may expose the agent to consequences that are too negative when choosing low value actions. A compromise is to choose each action with a probability that is proportional to the value of the action. This principle is captured by the *softmax action selection rule* (Dayan & Abbott, 2001).

### Model-Free Versus Model-Based Learning

The learning rules we have considered so far are simple and powerful. Moreover, they can be adapted easily to explain an even wider range of learning phenomena. For example, they can accommodate generalization learning through a modification of the update rule, such that not only the value of the presented stimulus (or chosen action) but also the values of not presented stimuli (non-chosen actions) as a function of the similarity (relation) between them and the presented stimulus (chosen action) are updated (Kahnt et al., 2012).

The rules considered so far are *model-free* in the sense that learning relies on exposure to outcomes and their predictions, given states and actions, without an understanding of how one state or action leads to another state. However, this blindness to the causal structure of the environment produces slow learning and inflexible behavior when the environment or the goals of the agent change, which may be particularly vexing in cultural contexts.

*Model-based* rules circumvent the shortcomings of model-free rules by learning the structure of how states or actions lead to other states. In a typical example (Tolman, 1948), a rat would explore a maze in the absence of reward (similar to person B studying the map of Beijing before moving). If reward is subsequently introduced at a specific location in the maze (person B hears about a good restaurant after moving), the rat can plan its route and learn more quickly than without previous experience of the maze, suggesting that it has acquired a mental model of the maze. Formally, model-based algorithms also use prediction errors, but these concern states rather than rewards. State prediction errors, weighted by a learning rate, serve to update the predictions of state transitions (Glascher, Daw, Dayan, & O'Doherty, 2010).

Note that model-free and model-based learning are not mutually exclusive and indeed usually occur simultaneously, with the relative weighting depending on learning history and situational factors such as the rate with which the environment changes (volatility). Moreover, the minimization of uncertainty or the optimization of costs and benefits may determine the degree to which learning agents rely on one or the other mechanism.

The distinction between model-based and model-free learning (at least partly) coincides with the distinction between *goal-directed actions* and *habits*. Goal-directed behavior is formally defined by sensitivity to the value of the outcome and is typically tested in situations in which that value changes (Dickinson & Balleine, 2002). Consider, for example, a rat that has learned to press a lever to obtain pellets. On one particular day, it is satiated on these pellets before being brought to the lab. Will it nevertheless press the lever? If yes, the behavior is a habit: The presence of the lever is sufficient to elicit a response even though the outcome is no longer valuable. If no, the behavior is goal-directed: The rat has a mental model that pressing the lever will produce an outcome with little value. In our example (Figure 5.2F), a model-based mechanism can help the bicultural agent to adaptively change her responses according to context.

### Neural Correlates of Learning and Risk Processing: The Role of Dopamine

The activity of a wide variety of neurons appears to encode elements of formal learning rules (Schultz & Dickinson, 2000). A particularly well-documented example comes from a group of neurons, located in the midbrain, that produce the neurotransmitter dopamine. In a variety of species, including humans, these dopamine neurons are activated by unpredicted but not by predicted reward and are depressed when predicted reward is unpredictably withheld (Montague, Dayan, & Sejnowski, 1996; Schultz, Dayan, & Montague, 1997; Zaghloul et al., 2009). Thus, the activity of these neurons reflects reward prediction errors. It does so with quantitative precision across many levels of prediction errors (Bayer & Glimcher, 2005; Enomoto et al., 2011; Fiorillo, Tobler, & Schultz, 2003; Tobler, Fiorillo, & Schultz, 2005). Moreover, during learning, activity transfers from the time of the reward delivery to the time of reward-predicting stimuli, such that the earliest reward-predicting stimulus, but not subsequent stimuli predicted by it, activates dopamine neurons (Schultz, Apicella, & Ljungberg, 1993). Thus, activity elicited by reward predictive states can itself reinforce activity to earlier states, exactly as suggested by the TDlearning account of second (and higher)-order conditioning.

Traditionally, dopamine neurons have been thought to incorporate model-free learning mechanisms. However, at least some evidence suggests that they may also play a role in model-based learning (Nakahara, Itoh, Kawagoe, Takikawa, & Hikosaka, 2004; Satoh, Nakai, Sato, & Kimura, 2003). Some of this evidence comes from a task in which the values of two stimuli are anticorrelated such that they both reverse simultaneously (Bromberg-Martin, Matsumoto, Nakahara, & Hikosaka, 2010). As soon as the agent has realized that the value of one stimulus has changed, she can infer that the value of the other stimulus has also changed without having to experience the outcome of that stimulus. Both behavior and dopamine neurons process inferred outcome values, although the impact of experienced value on both is more pronounced. In particular, dopamine neurons respond more strongly to a stimulus that is inferred to be valuable than to a stimulus that is inferred to be nonvaluable. This is compatible with the idea that dopamine neurons receive model-based information, but note that similar findings could also arise with a modification of model-free learning.

Dopamine neurons fire as if they emit a prediction error signal at each moment in time. However, they are sensitive not only to the mean but also to the variance of the prediction. In particular, a slower response increases with the predicted variance of the reward outcomes (Fiorillo et al., 2003). Moreover, the prediction error response adjusts sensitivity to that variance (Tobler, et al., 2005). This adaptive response may optimize learning depending on the properties of the environment and may be particularly useful when moving from one culture to another.

All the described properties of dopamine neurons have been found also with human neuroimaging, particularly in target regions of dopamine neurons, such as the striatum and the frontal cortex. Hemodynamic activity in the striatum, for instance, shows prediction errors (McClure, Berns, & Montague, 2003), response transfer (O'Doherty, Critchley, Deichmann, & Dolan, 2003), higher-order conditioning (Seymour et al., 2004; Tobler, Fletcher, Bullmore, & Schultz, 2007), risk responses (Preuschoff, Bossaerts, & Quartz, 2006), and adaptation (Park et al., 2012); for review, see Daw and Tobler (2013) and Tobler and Weber (2013).

## Risk: Neuroscience and Culture

In recent years, a comprehensive research program examining the neural correlates of decision-making in risky and/or uncertain environments has uncovered a network of interrelated areas. Risk and its aspects seem to be encoded not only in the striatum but also in the anterior insula, anterior cingulate, dorsomedial and dorsolateral prefrontal cortex, and inferior parietal lobule (Burke & Tobler, 2011; Christopoulos, Tobler, Bossaerts, Dolan, & Schultz, 2009; Huettel, Song, & McCarthy, 2005; Huettel, Stowe, Gordon, Warner, & Platt, 2006; Knutson, Wimmer, Kuhnen, & Winkielman, 2008; Kuhnen & Knutson, 2005; Levy, Snell, Nelson, Rustichini, & Glimcher, 2010; McCoy, Crowley, Haghighian, Dean, & Platt, 2003; Schultz et al., 2008; Tobler, Christopoulos, O'Doherty, Dolan, & Schultz, 2009). Our work has demonstrated that risk can be processed subjectively even in conditions in which choice is not required (Christopoulos et al., 2009; Tobler, Christopoulos, O'Doherty, Dolan, & Schultz, 2008). By extension, given that people are typically risk averse and given that culture may reduce risk it is conceivable that culture positively affects the well-being of people even at times when they do not have to make risky choices.

Culture seems to impact or interact with risk preferences, but the exact mechanism is largely unknown. Hofstede (1980) early on recognized uncertainty avoidance as one of the main dimensions that characterize cultures. In a pioneering study, Weber and Hsee (1998) suggest that differences in decision-making across cultures are mostly provoked by differences in the *perception* of risk rather than attitudes toward risk itself. Still, large-scale studies have confirmed that risk attitudes do differ across countries and that these attitudes correlate with both macroeconomic indicators and cultural parameters (Rieger, Wang, & Hens, 2011; Vieider, Chmura, & Martinsson, 2012). Typically, Asian (and collectivistic) cultures seem to be less risk averse (Bontempo, Bottom, & Weber, 1997; Bruhin, Fehr-Duda, & Epper, 2010), with the "cushion hypothesis" (i.e., the presence of a social network that can protect from losses) being one potential explanation (for a review and some objections, see Ji &Kaulius, 2013). In addition, cultural processes and influences could function as a buffer to risk-taking behavior (e.g., see Chapter 14).

In addition to these arguments, one should not forget that risk preferences (and therefore, indirectly, the tendency for exploration and niche construction) could be transmitted both genetically and culturally. Indeed, genetic factors are implicated in risky decision-making (Kuhnen & Chiao, 2009) and twin studies in China and Sweden support the contribution of genetic factors in the transmission of risk preferences (Cesarini, Dawes, Johannesson, Lichtenstein, & Wallace, 2009; Zhong et al., 2009). Monocultural studies also point to the intergenerational transmission of risk preferences (Dohmen et al., 2011; Kimball, Sahm, & Shapiro, 2009).

## Social Learning: Translating RL and Valuation to Sociocultural Phenomena

Previously, we described how agents update values and decide in dynamic environments. However, in many of the examples mentioned so far, the environments were asocial—that is, the agents were interacting with nature only.

During the past few years, the same framework has been used to explain how humans learn and decide when they dynamically interact with other humans. Obviously, there are substantial differences between interacting with nature or humans (e.g., recognizing that choices are signaling intentions and therefore might serve more general or long-term strategic goals). However, this fact does not at all preclude employing RL mechanisms to learn and update choices also in interactions with strategic conspecifics.

Here, we review behavioral and neuroscience evidence that describes the role of adaptive learning mechanisms in three critical sociocultural phenomena: observational learning, strategic interactions, and niche construction.

### *Observational Learning*

Not only the physical but also the social environment can be the object and the source of learning processes. Through observing others, we can gain valuable information about states and state transitions at lowcost and without having to experience them all ourselves. This strategy offers obvious advantages not only in terms of economy but also in terms of transmission of successful strategies within groups.

Instructing others may help establish and perpetuate cultural practices. Given the ubiquity and success of prediction errors in explaining individual learning, it may not come as a surprise that they also feature heavily in explanations of social associative learning. Indeed, a variety of such prediction error signals have been investigated, including the difference between one's predictions of one's own outcomes and the actual social outcome (Burke, Tobler, Baddeley, & Schultz, 2010), the difference between one's prediction of another's outcome and the actual social outcome (Seid-Fatemi & Tobler, 2015; Suzuki et al., 2012), the difference between one's own probability of choosing an action and the actually observed social action (Burke, Tobler, Baddeley, et al., 2010), the difference between one's prediction of another's action and the actually observed social action (Behrens, Hunt, Woolrich, & Rushworth, 2008; Hampton, Bossaerts, & O'Doherty, 2008; Suzuki et al., 2012; Zhu, Mathewson, & Hsu, 2012), and the difference between one's prediction of one's influence on others and the actual influence (Hampton et al., 2008). Thus, the degree to which social information enters into the calculation of the prediction error can vary, again illustrating the versatility of prediction error-based learning. At the neural level, regions of medial prefrontal cortex have been implicated primarily in underpinning these various forms of social learning.

The actions of others typically influence the actions of an agent in a conforming manner. For example, knowing that others like a particular face or piece of music and that others have bought a particular stock increases our own liking of that face (Klucharev, Hytonen, Rijpkema, Smidts, & Fernandez, 2009) or piece of music (Campbell-Meiklejohn, Bach, Roepstorff, Dolan, & Frith, 2010) and propensity to buy that stock (Burke, Tobler, Schultz, & Baddeley, 2010). A recent study suggested that the mere observation of other's choices overdifferent gambles increases the utility of the selected gamble; this socially mediated utility is represented in ventro-medial prefrontal cortex and this neural signal predicted conformity (Chung et al., 2015). When moving from one culture to another, such conforming influences may be particularly prevalent, and social learning mechanisms can help implement them (see later). Moreover, previous expectations about others (Delgado, Frank, & Phelps, 2005) or advice from others (Biele, Rieskamp, Krugel, & Heekeren, 2011) may bias one's actions and learning processes even in the absence of others behaving differently.

### *Strategic Interactions*

When people interact with members of the same or a different cultural group, they need to learn what is expected and standard. For instance, to what extent do people reciprocate, trust, and cooperate? How do they allocate resources? This information can be, to some extent, transmitted linguistically; however, everyday experiences and interactions could be more informative and potentially have a higher impact on behavior. Therefore, it is useful to understand how humans update the representations of such social norms as a function of repeated interactions with the same or different social actors.

Behavioral game theory (Camerer, 2003) offers a convenient framework to study such social interactions. In these experiments, two or more participants are engaged in a well-structured social exchange, with more or less specific roles. Usually, the agents are endowed with specific monetary rewards that they can choose to spend when interacting with the other agent(s). The advantages of this approach are numerous:(1) The rules of the social exchange can be defined at will, such that choices reveal specific strategic preferences (e.g., cooperation); (2) the setup allows for studying *behaviors* and *actions* instead of attitudes and opinions; (3) the tasks can be dynamic—that is, they can allow for many repeated interactions, thus well simulating real-life environments (contrary to traditional, more "static" social psychology approaches); and (4) they are computationally tractable, allowing for fitting of both behavior and neuronal responses (an extensive review of neuroimaging tasks studying social cognition is provided by Phua and Christopoulos (2013)).

Learning plays a role also in these situations. One of the first demonstrations of a prediction-error signal in strategic interactions was described by King-Casas et al. (2005, 2008). Pairs of participants repeatedly played the trust game (Berg, Dickhaut, & Mccabe, 1995; Klucharev et al., 2009): In this experimental setup, the monetary amounts exchanged represent trust and reciprocity signals. Critically, each subject had to "learn" what the intentions of the partner were and accordingly update his or her expectations. As described previously, in nonsocial reinforcement learning experiments, unpredicted rewards produce prediction errors; in a similar way, unpredicted rewards for oneself produced by social gestures in the trust game were signaled by responses in ventral striatum. Critically, caudate responses showed a temporal transfer from the time point that the decision of the partner (and the associated reward) was revealed (reactive responses) to the earlier time of deciding how much to trust the partner (representing a predictive signal).

Reinforcement learning appears to play a role also when one learns the norm of a group. It has been suggested (Klucharev et al., 2009) that prediction error signals appear when one compares one's opinion with the opinion of the group. Striatal responses represent the discrepancy between the agent's behavior and the behavior of the group. In the experiment by Klucharev and colleagues, participants were asked to rate a face in terms of attractiveness; subsequently, they were presented with the (mean) group rating of the very same face. Discrepancies between the group and the personal opinion were associated with "prediction error"-like responses in rostral cingulate and nucleus accumbens. Interestingly, these signals appear to subserve conformity mechanisms. The authors asked participants to re-evaluate the faces after the experiment. Faces that had higher cingulate response and lower nucleus accumbens activation during the first phase were more likely to be re-rated in accordance with the mean rating of the group, thus suggesting a conformity signal.

Albeit useful, pure RL strategies are incomplete and inefficient in strategic environments. This is because an agent that only employs RL strategies does not take into account the possibility that other social actors could adopt strategies that exploit them. To face this possibility, it is suggested (Camerer, 2003; Sutton & Barto, 1988) that organisms employ *belief-based learning*. This avenue of learning suggests that the decision-maker learns and incorporates the structure of the game (or, more generally, the structure of the situation) in the value-updating algorithm, analogous, to some extent, to model-based learning. Thus, agents need to form and dynamically update their beliefs (Fudenberg & Levine, 1998) about the actions and strategies of their opponents before deciding on their own actions.

Belief-based learning is also based on prediction error computations (appearing while the agent is updating beliefs about the strategies of the opponent); however, these belief-based prediction errors can be computationally distinct from the prototypical RL prediction errors, which only update values attached to actions or stimuli (and not to strategies). Zhu et al. (2012) examined whether the RL framework can be extended to belief learning. They found that whereas the ventral striatum seems to subserve both types of learning, rostral anterior cingulate cortex uniquely signals *belief-based* prediction error computations. In fact, behavioral and computational analyses suggested that the participants used both learning algorithms because a hybrid model combining RL and belief-based learning outperformed models that were solely based on either type of learning.

Social life often could benefit from advice or information provided directly by other agents (note that such teaching and instruction is different from observational learning). This is a capability that is comparably well developed in humans, in whom linguistic tools can serve the function of advice-giving. However, the decision-maker needs to evaluate the value and the trustworthiness of the advisor, who—for strategic or other reasons—might offer unreliable recommendations. Behrens and colleagues (2008) developed an experimental paradigm in which participants were asked to make decisions in a changing environment. Concurrently, participants received advice from trustworthy or untrustworthy partners. Therefore, participants needed to update the stochastic properties of (1) the nonsocial environment (i.e., the outcomes of the decisions as they were determined by nature) and (2) the social environment (i.e., the reliability of the advisor). The two processes were subserved by distinct areas both located in the dorsal anterior cingulate cortex. Ventromedial prefrontal cortex seemed to combine the two types of information.

The anterior insula has been implicated with assessing negative rewards (Kuhnen & Knutson, 2005; Palminteri, Clair, Mallet, & Pessiglione, 2012); risk and risk prediction error (Burke & Tobler, 2011; Burke, Brunger, Kahnt, Park, & Tobler, 2013; Ishii, Ohara, Tobler, Tsutsui, & Iijima, 2012; Mohr, Biele, & Heekeren, 2010; Preuschoff, Quartz, & Bossaerts, 2008); and, from a more general standpoint, with monitoring visceral and autonomic responses to external stimuli, especially painful or disgusting ones (Critchley, Elliott, Mathias, & Dolan, 2000). It is not surprising that this area is also signaling socially undesirable actions such as social exclusion (Bolling et al., 2011; Lamm, Decety, & Singer, 2011; Meyer et al., 2013) and pain of a loved one (Singer et al., 2004). Within strategic interactions, the anterior insula is activated by a form of free riding (unreciprocated cooperation) (Rilling et al., 2008) and receiving unfair offers in the ultimatum game (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). Both cases could be conceived of as negative prediction errors because the actions of the social partner offer rewards that are smaller than what is normatively expected.

In summary, during successful—or at least satisfactory—execution of strategic interactions, agents need to constantly update the values attached to different actions and beliefs about other agents. There are two main reasons that drive this necessity. First, agents understand that the world is changing, which means that they need to regularly update their expectations. Second, the information agents have collected so far and/or the way it has been structured contains a more or less significant amount of uncertainty. This uncertainty can be managed by constantly updating the expectations and beliefs associated with the environment—social and nonsocial. With each new piece of information, agents decide to what degree it should impact current predictions. An extreme outcome should receive more weight instable and certain environments than in unstable and uncertain environments. Thus, the learning rate may itself be learned, which results in hierarchical learning architectures (Behrens, Woolrich, Walton, & Rushworth, 2007; Frank & Badre, 2012; Mathys, Daunizeau, Friston, & Stephan, 2011; Payzan-LeNestour, Dunne, Bossaerts, & O'Doherty, 2013).

## Genetic Contributions

Recent research has provided evidence on the genetic basis of learning and strategic interactions. The topic is too broad to discuss here, but we refer to two important genes; we later discuss the impact of these genes in socioculture research. The enzyme catechol-*O*-methyltransferase (COMT) regulates extrasynaptical dopamine degradation (Malhotra et al., 2002). Individuals homozygous for the methionine (Met) allele of the Val$^{158}$Met polymorphism in COMT have lower COMT activity and higher levels of dopamine in prefrontal cortex compared to homozygotes for the valine (Val) allele (Barnett, 2011; Egan et al., 2001). Val homozygotes seem to perform better in a reversal-learning task (Krugel, Biele, Mohr, Li, & Heekeren, 2009), possibly because their anticipatory reward responses are reduced, at least in gambling tasks (Yacubian et al., 2007). Note, however, that there can also be curvilinear relations between dopamine levels and performance (Cools & D'Esposito, 2011). DRD2 is another gene that seems to regulate dopaminergic functions. Individuals with a specific polymorphism (at least one T allele at the *Taq1A* single nucleotide polymorphism) have fewer D2 dopamine receptors (compared to carriers of CC alleles) (Blum et al., 1995; Noble, Blum, Ritchie, Montgomery, & Sheridan, 1991). Behaviorally, this seems to be translated into aggression and impulsivity (Blum et al., 1995). For more studies on the genetic basis of dopamine-mediated learning, see Frank, Doll, Oas-Terpstra, and Moreno (2009) and Klein et al. (2007).

## From the Jungle to New York: Understanding Nature Versus Understanding Culture

The reviewed neuroscientific studies, along with others (Delgado et al., 2005; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004), highlight the role of various brain structures, such as the mesencephalic dopamine projections, and particularly medial prefrontal cortex, in dynamic social decision-making. They also demonstrate that precisely defined computational terms can explain both brain activity and choice behavior in rather complex tasks and situations.

Our framework poses a major underlying research question: *To what extent are the mechanisms and skills that humans employ to understand the stochastic properties of nature are also used to interpret the social environment*? This question is still unresolved, and it seems that culture neuroscience can be informed from and inform this research agenda, as it will be explained later.

Conceptually, it should be expected that cognitive mechanisms employed to understand nature's complexity would also be used in social exchanges. One reason is that both the social and the natural environment behave in a probabilistic manner and therefore developing new or specialized monitoring functions and computational mechanisms would be partially redundant (Rilling, King-Casas, & Sanfey, 2008). However, social exchanges have some particularities that might make such mechanisms insufficient. A principal characteristic is that social agents are or could be strategic in their behavior, thus making the problem nonstationary (Rilling, King-Casas, et al., 2008). By consequence, the choice and value of an action become contingent on the actions of other agents (which rarely is the case with nature). Responses performed by social partners could represent higher-order strategies, aims, or preferences that pure reinforcement learning strategies might fail or be very slow in recognizing and appropriately responding to. Moreover, a social agent who behaves according to reinforcement learning rules might eventually be very predictable, which could be disadvantageous in antagonistic environments (but possibly advantageous in cooperative environments).

Critically, social agents might aim at maximizing not just their own well-being but also that of other agents. From a more general viewpoint, social agents incorporate the outcomes received by others in their decision mechanisms. Such preferences have been examined under concepts such as social value orientation, spitefulness, reciprocity, and altruism (Bolton & Ockenfels, 2000; Christopoulos & King-Casas, 2015; Fehr & Schmidt, 1999; Haruno & Frith, 2010; Rabin, 1993; Van Lange, Otten, De Bruin, & Joireman, 1997). Within that framework, choices are evaluated not only according to the outcomes received by the decision-maker herself but also as a function of the outcomes received by other agents. For instance, cooperative agents might prefer actions that maximize the sum of their own and another agent's outcomes (e.g., $70 for the decision-maker and $70 for another person) over actions that only maximize their own outcomes (e.g., $100 for the decision-maker and $10 for the other person). Moreover, equality or equity preferences or competitive idiosyncrasies could influence the decision process (Falk, Fehr, & Fischbacher, 2003; Fischbacher, Falk, & Fehr, 2008).

Choices in a social environment not only express preferences of the agent but also can be used as *signals* of preferences and properties for and by other agents. Therefore, the value of a choice is determined not only by the outcomes produced but also by the information that can be used to transmit future intentions and strategies. Moreover, such information can be more or less valuable depending on how outcomes are generated. For example, signaling may be more important and enhance the value of outcomes when outcomes are produced by skill rather than luck because skill provides information about the signaler, whereas luck does not (Vostroknutov, Tobler, & Rustichini, 2012). Hence, a socially astute organism should include the informational value of a choice into its decision process.

From a neuroscience perspective, there is evidence of systems specialized in monitoring and valuing dynamic and volatile social exchanges. As previously mentioned, Behrens and colleagues (2008) found structurally discreet responses in the anterior cingulate cortex for social and nonsocial volatility. Rilling et al. (2002) also noted that rewards that are received as a result of interactions with a human partner as opposed to a computer have both common and distinct neuronal representations. Recent work suggests that social preferences over different allocations of money (mirroring competitive or cooperative outcomes) could be employed during dynamic interactions requiring learning (Christopoulos & King-Casas, 2015); these learning computations are represented in the medial prefrontal cortex and are thus neuronally and computationally distinct from typical reinforcement learning signals when in nonsocial environments. Moreover, social prediction errors appear to be coded in more dorsal regions of medial prefrontal cortex than individual prediction errors (Seid-Fatemi & Tobler, 2015). On the other hand, there is evidence that striatal and amygdala responses are mediating sensitivity to betrayal aversion, a form of social risk aversion (Lauharatanahirun, Christopoulos, & King-Casas, 2012). Finally, signals in the temporoparietal cortex contain more information about upcoming decisions when subjects play poker against human compared to computer opponents (Carter et a., 2012). These studies suggest that special mechanisms (subserved by distinct brain regions) might have been developed to monitor the social environment (as opposed to the natural environment).

## From New York to Beijing and Around the World: Using Principles of Learning Theory to Understand Culture and Vice Versa

The previous discussion suggested that basic learning and valuation mechanisms can be used in social environments and exchanges, if appropriately specialized and modified. It is therefore an open question whether these basic social learning mechanisms can be further tuned to culture, particularly to specifically cultural characteristics or in situations in which culture has a dominant role. In the introduction, we suggested that culture could have a decisive function by determining the stochastic properties of the social environment. As a conclusion, we offer a general, dynamic, but rather speculative framework that relates cultural phenomena to the computational and neurobiological accounts of learning.

### *Tight Versus Loose Cultures*

Gelfand et al. (2011) identified the "tightness" of a culture as a predominant dimension characterizing cultural diversity. Interestingly, the authors consider ecological and historical threats to be one of the main sources of this differentiation. The tightness concept refers to the distribution of allowable or punishable behaviors. Translating this to pure statistical terms, one could speculate that agents in tighter cultures are experiencing, choosing from, or observing a relatively narrow distribution of behaviors. In other words, the space of available actions is culturally restricted (Figure 5.1).

A question is how members of these two cultural types, as well as cultures in general, learn in such environments. An RL-based computational account would predict that in tighter environments, learning could be faster because there is less uncertainty on what is rewarded and what is punishable. Observational learning would also be more efficient because the probability that observed behavior is representative of the culture is higher.

On the other hand, this tightness could be disadvantageous because it provides strong incentives against deviations and, conceivably, explorative actions. The effect of punishment could be further strengthened in two ways: The punishment could be heavy and also very probable. Such restrictions would punish general exploratory endeavors, even in other domains, possibly via a mechanism of generalization.

### *Learning and Relearning: Response to Change*

The problem of dealing with uncertainty might become exacerbated in the modern world, which is characterized by increased volatility, changes, and instability. In such cases, members of cultures need to update the stochastic properties of their beliefs and expectations and revise the associated probability distributions.

The RL framework would predict that these responses could be mediated by at least two mechanisms. The first mechanism (*model-free*) will employ basic RL to slowly update the predictions based on experienced outcomes, resulting inacquisition, extinction, and reversal learning. This mechanism is reliable and eventually leads to habit formation; however, it is slow to update and most likely inefficient in very volatile environments. It can therefore also become a source of resistance to change.

As noted, recent advances in the neurobiology of learning suggest that in volatile environments or with changing goals, agents can employ another mechanism—*model-based* learning. This type of learning is faster and more versatile because it can update beliefs and represent state transitions. Therefore, in volatile or parallel but switching environments, model-based learning mechanisms may be more adaptive.

### *Niche Construction*

Human and, to a lesser extent, animal cultures have the ability to produce and transmit information to other members via niche construction or, in other words, via the modification of the environment. Evolutionary approaches (Gintis, 2011; Laland, Odling-Smee, & Feldman, 1999) posit that this modification of the environment is one way (the alternative way is genetic transmission) for successful information transmission Gintis, 2011). Notice that the direction of the transmission could be both vertical (from generation to generation) and horizontal (from one group to another group). Moreover, gene–culture coevolution allows for cumulative growth across and even within generations and contributes to the development of basic social skills, such as reciprocity and cooperation (Ihara, 2011; Zajonc, 1984; for review, see Gintis, 2011).

The successful adoption of niches necessitates that members undergo *socialization* (Laland et al., 1999) (see also the later discussion on the integration of socialization to the current framework). Gintis (2003, 2011) suggests that the whole internalization mechanism is genetically predisposed; however, the details of this process have not yet been described. It could be argued and tested that internalization of norms is partially learned (through acquisition of reward and punishment predictions, observational learning, interaction between model-based and model-free learning, as well as the balance of goal-directed and habitual behavior). Internalization of norms usually happens by repeated interactions between the younger and older generations. Here, genetic and neurological differences could determine susceptibility to socialization. However, niche construction by the younger generation would possibly necessitate explorative actions and reliance on model-based learning, which is more flexible to respond to changes.

Learning and niche construction play a significant interdependent role during socialization, especially during childhood. The alterations in the environment that niche construction imposes not only influence the selection of genes but also channel, facilitate, or even limit the learning opportunities offered to the younger generation (Flynn, Laland, Kendal, & Kendal, 2013; Wheeler & Clark, 2008). This theorization highlights the fact that not only what we learn but *also how we learn is largely shaped by the cultural environment*. Mathematical modeling has been successfully employed to simulate socio evolutionary dynamics of niche construction (Lehmann, 2008). Therefore, we are faced with an exciting opportunity for combining the computational aspects of basic learning mechanisms and socio evolutionary processes to form a multilevel explanation of cultural phenomena. These analyses can even address biological phenomena at the level of neurotransmitters; for instance, dopamine release and function, as the main force behind motivation and learning, could monitor and initiate niche construction (Li, 2013).

### *Biculturalism, Polymorphic Populations, and Cultural Mixing: Dynamic Constructivist Approach*

A popular account modeling cultural mechanisms is the dynamic constructivist approach (Hong, Morris, Chiu, & Benet-Martinez, 2000). Its principles explain in a comprehensive way the mechanisms with which bicultural individuals adapt to different cultures. The basic idea is that bicultural individuals are able to switch their "cultural frames" and accordingly adapt their behavior and expectations.

This phenomenon is interesting from a RL standpoint because it suggests that individuals can base their behavior on more than one probability distribution. In the experiments by Hong et al (Hong et al., 2000; Wong & Hong, 2005), switching behavior was found to be relatively easily and quickly induced. This might imply the testable hypothesis that cultural switching is subserved by model-based learning mechanisms and their associated structures. Understanding the exact mechanism could help us explain and even predict the effects of cultural mixing, where more than one model (or *schema*) can be engaged depending on environmental stimuli. For example, when cultures are of different tightness, agents may flexibly employ different learning rates. Moreover, it could also be tested whether cultural intelligence (Earley & Ang, 2003), which loosely refers to the ability to adapt to different cultures, is related to reversal learning abilities.

Another critical implication is the relationship of genetic and behavioral variability in a population. Different humans have different genetic backgrounds; moreover, different groups of people have different distributions of genes. For instance, collective cultures have more carriers of the serotonin transporter functional polymorphism (5-HTTLPR) (Chiao & Blizinsky, 2010). Following the niche construction approach, this variability could be the outcome of a bidirectional exchange between biological and cultural processes. With respect to dopamine, variations in dopamine-related genes could reflect and be an outcome of cultural responses to a changing environment. For instance, variation in dopamine D4 receptor allele frequencies has been associated with migratory patterns of different populations (Chen, Burton, Greenberger, & Dmitrieva, 1999). The combination of basic learning theory with the knowledge of population genetics could help in further elucidating the gene–culture interaction in a dynamic manner.

### *Social Learning, Imitation, and Reinforcement Learning*

Related to the previous discussion is the question of how cultural learning (i.e., the adoption of cultural parameters) is computationally and cognitively realized. Cultural learning and cultural transmission are massively based on imitative learning (Sommerville & Decety, 2006; Tomasello, Savage-Rumbaugh, & Kruger, 1993), and its main characteristic is that it is largely social in the sense that it necessitates the interaction of two or more agents. At least in captivity, chimpanzees can employ imitation, even when only visual contact is allowed (Whiten et al., 2007). Furthermore, overimitation in young children might be universal (Nielsen & Tomaselli, 2010).

Initial accounts of social and imitative learning (Boyd & Richerson, 1985; McElreath, 2004) seem to differentiate these forms of learning from individual learning. According to this viewpoint, imitative learning is an alternative to individual learning and is adopted when individual learning is inefficient, especially in terms of cost and accuracy. However, other accounts described later (including our proposed framework described here) suggest that imitative learning can—at least partially—employ reinforcement learning mechanisms; in fact, successful imitative learning sometimes *has to* employ reinforcement learning. In the following, we offer a number of arguments for this statement.

First, in accordance with Castro and Toro (2004), imitation is not blind to evaluative processes. Discovering and learning a novel behavior provide only the very first steps of imitation; in order to be incorporated permanently in the behavioral repertoire, imitative learning requires that the learned behavior is tested and evaluated and sometimes changed ("guided variation"; Boyd & Richerson, 1985). These crucial steps imply the existence of mechanisms, with which the value of learned actions is evaluated and updated, most likely via the production of prediction errors. This is further supported by Iacobini (2009), who identifies two main neurocognitive systems for imitation mechanisms: the associative sequence-learning model (which is a form of experience-based Hebbian learning) and the ideomotor framework (which emphasizes the overlap of observation and execution).

Consider, for instance, the example of a hominid discovering a new fruit and tasting it. Another hominid is observing the action and learns how to harvest and eat the fruit. The second hominid would need to update the value of the action according to her predictions and the value of the fruit. If such an updating mechanism were absent, then imitative learning would be short-lived.

Critically, in this example, it is not only the action of harvesting the specific fruit that is updated but also the value of observing the actions of the first hominid. If the fruit is nice, then the first hominid acquires added value in the eyes of the second hominid. This is very similar to the experiment in which reinforcement learning mechanisms were adopted to assess the reliability of an advisor (Behrens et al., 2008). Indeed, higher value could be attached not only to the first hominid but also to the general action of observing and imitating. Tomasello and colleagues (Tomasello, Carpenter, Call, Behne, & Moll, 2005) go further in suggesting that cultural learning is a primary reinforcer in itself, meaning that an agent would derive value simply from imitating an action.

Finally, imitation is largely based on reward and punishment mechanisms. Especially for humans, the ability of the older generation to punish and reward offspring behavior seems to be a major determinant of successful imitative learning and, in general, cultural transmission (Castro & Toro, 2004).

### *Socialization, Generalization of Stereotypes, and Enculturation*

Our framework can explain enculturation via the mechanisms of cultural mixing, niche construction, and social learning and relearning of norms. Additional applications exist, such as anticipatory socialization (Merton & Rossi, 1950)—that is, how individuals adopt the norms and rules of groups that they aspire to join. This process might be to a great extent subserved by observational learning and imitation mechanisms and in many cases might involve reversal learning. A typical example is the adoption of gender (maternal) roles by young girls. Another example is the role of reinforcement to the various stages of socialization (Moreland & Levine, 1982). Of particular interest is the stage of *maintenance*, in which the individual might need to negotiate his role and adopt new rules; here, learning mechanisms such as extinction and reacquisition might play a significant role. Notice also that generalization seems to be a key mechanism in stereotype formation, and more studies are needed to examine the phenomenon under the RL framework (Brown & Hewstone, 2005). Finally, excessive failures of socialization as demonstrated in the cases of antisocial behavior could be employed (Snyder et al., 1997).

### *Enculturation Across the Lifespan*

Many studies have provided evidence that dopamine function and levels change (in many cases decline) across different stages of life (Li, Lindenberger, & Backman, 2010; Lindenberger et al., 2008), potentially related to genetic variability (Hammerer et al., 2013). It is therefore expected that such alterations might also influence social learning and enculturation. The association between levels of dopamine and critical functions such as attention, learning, and working memory (Nagel et al., 2008) could, in turn, mediate resistance to change, speed of learning, and effective observational learning—functions that are all involved in enculturation. Thus, it might be worthwhile to relate the effect of such molecular-level changes to macro-responses; for instance, will changing demographics (aging)—and the associated changes at molecular levels, such as the distribution of dopamine receptors—influence cultural responses to change?

### *Culture and Learning Parameters*

The effect of culture or culture-related parameters on learning and, in general, adaptive responses is largely unexplored. Previous studies have demonstrated that cultural parameters such as individualism–collectivism (Chiao et al., 2009, 2010), social dominance (Chiao, Mathur, Harada, & Lipke, 2009), or social power (Harada, Bridge, & Chiao, 2012) seem to influence elements of cognition. Future research could examine how these parameters affect learning, at both a behavioral and a neuronal level, and whether cultures differ in terms of optimal learning parameters.

### *Social Learning and Psychiatry*

The symptomatology of many psychiatric illnesses, including personality disorders, autism, depression, and psychosis, is characterized by marked deficits in social interactions. For instance, unstable relationships and oversensitivity to rejection characterize borderline personality disorders (Arntz, 2005; King-Casas et al., 2008); early and late-onset psychosis is characterized by difficulties in many areas of social life, such as a high probability of a divorce, difficulty establishing and maintaining social relationships, mistrust and suspicion, and a major need for autonomy (Almeida, Howard, Levy, & David, 1995; Howard, Almeida, & Levy, 1994; Howard & Levy, 1992), and is largely mediated by presynaptic striatal dopamine dysregulation (Howes & Kapur, 2009; Tan & Weinberger, 2010). However, studies, especially in late-onset psychosis, are mostly based on Western samples. The present framework could uncover how miscalculations during learning of the social environment could underlie social deficits in various cultures. For example, such social deficits could be supported by inappropriate representation of "social" prediction errors (e.g., when violations of trust are overweighted) (Behrens, Hunt, & Rushworth, 2009; King-Casas & Chiu, 2012). Here, the cultural factor is critical because different cultures have different expectations and thus violations would be computationally distinct from culture to culture. This variability, which, as discussed, reflects an interaction between genetic, environmental, and cultural factors, could also facilitate the understanding of major differences in the symptomatology, prevalence, expression, and diathesis of various psychiatric disorders across different cultures.

In summary, RL mechanisms appear to provide promising and far-reaching but largely unexplored avenues for future culture research. In particular, it remains to be tested whether and how RL mechanisms can contribute to various types of social learning, as well as whether there are specialized systems for reinforcing imitation of evolutionary or socially fitter social actors.

## Understanding Responses to Uncertainty: Computational Cognitive Neuroscience

In a similar way that learning and other dynamic phenomena have been examined with computational approaches, the study of sociocultural phenomena will also benefit from the employment of computational approaches. Here, we briefly list a number of theoretical and practical/methodological considerations that can allow for such an approach:

1. A common attribute of the phenomena described previously is that they are inherently *dynamic*. This means that it is quite difficult, if not meaningless, to study them in a static environment. In order to understand learning and responses to uncertainty, the participants will need to actually learn during the experiments, in an environment that is largely stochastic. For that reason, the experiments will benefit from including choices or passive viewing of stimuli that produce outcomes in a nondeterministic manner. Participants need to uncover the stochastic properties of the experiment themselves by experiencing the outcomes of their choices.
2. A second useful property is to develop paradigms that are *interactive*—that is, they respond and adapt according to the previous choices of the participant. For example, in one of our experiments on risk (Christopoulos et al., 2009), the task parameters were updated depending on the choices of the participant to ensure equal subjective value of the different choice options; in game situations, a computer program can be preprogrammed to play with the subject according to specific strategies, thereby increasing experimental control compared to the case in which others interact with the participant in realtime. Of course, choosing to adopt such an experimental environment should be done carefully because it risks that the participant, consciously or not, could understand that the responses are artificial.
3. Computational modeling: Like many other parts of neuroscience, computational neuroscience assumes that choices and behavior in general are a function of some input parameters. Computational models specify how the behavioral output relates to the input in a mechanistic and formal way. In other words, on each trial, the properties of the input (e.g., the color of the stimulus, the risk of a gamble, the degree of social distance, or, in learning, the outcomes of previous trials) are combined in a function that essentially predicts some observable response (e.g., the behavioral or the brain response) in that specific trial. Based on that logic, a researcher can build two or more, usually competing, models that test different hypotheses (e.g., recall the study by Zhu and colleagues (2012), in which agents combined reinforcement and belief-based learning). These models can be tested against both behavioral and neuronal responses (Figures 5.3B and 5D).

Computational modeling will thus benefit from experiments in several ways. First, it is useful to measure a behavioral response in order to examine whether the assumed model can predict these responses to a satisfying level. This will provide more confidence in the plausibility of the model because brain responses tend to be noisy (Figure 5.3A). Second, it is also useful to employ multilevel conditions (e.g., many levels of social distance) and not just two levels (Figure 5.3A). This can uncover nonlinear responses. Finally, although not absolutely necessary, multimodal (rather than unimodal) stimuli can offer the possibility for uncovering hidden interactions between different parameters. For an excellent description of how to analyze trial-by-trial data using computational models, see Daw (2011).

Computational Culture Neuroscience is essentially an extension of computational approaches in neuroscience and social neuroscience. In that sense, there are many similarities: The approaches try to uncover hidden models of cognition that can connect in a formal (mathematical) form input parameters with behavioral and brain responses. This approach can explain the computations that could precede a choice and identify the brain structures whose responses resemble such calculations. In that way, cognition is parameterized, allowing for further specificity both in brain function and in psychological explanation.

The main uniqueness of computational culture neuroscience is that culture or cultural factors enter as separate parameters in the models, in addition to other psychological parameters. There are important questions to be answered in future studies in relation to that approach. One issue is that experimenters should consider whether different cultures employ the same models with different weights on the parameters (e.g., a culture overweighting negative outcomes when evaluating a risky prospect) or that different cultures have altogether different underlying models (e.g., a culture that has lexicographic rather than utility-based preferences over different prospects; Fishburn, 1975).

Moreover, it is an open issue how *prior expectations* of agents are dealt with. Although some computational models can incorporate these prior beliefs, it might occasionally be more advisable to create experiment-specific expectations (e.g., by having the participant interact with many cooperative agents before actually starting the main experiment). This implies the development of *experimental microcultures*. Finally, computational approaches have so far largely evaded employing narratives or other linguistic references to influence learning and adaptive responses. Narratives could be critical for affective and social or moral issues (Bridge, Chiao, & Paller, 2010); computationally, narratives might allow for quick model-based changes. It certainly remains a largely uncharted research field that is open to explore.

Group and individual differences can be identified with this approach, whereas the models can be extended to make predictions for completely different scenarios and situations. The main difference with traditional approaches is that the studies can uncover not only the behavioral differences but also critically the mechanisms or distortions that guide these differences. For instance, traditional approaches could reveal that people in a specific culture or group learn faster under certain conditions; however, a computational model could also identify the source of this difference (e.g., differential sensitivity to positive and negative outcomes; for example, see Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006) and thus make predictions for different scenarios and cases.

To summarize, Computational Cultural Neuroscience can provide insights into many different questions that are related to dynamic cultural phenomena. Different models of cognition can be fitted to both behavioral and neural responses to uncover hidden and difficult-to-identify parameters, such as trust and reciprocity, sensitivity to reward and losses, probability distortions, and sensitivity to different aspects of social distance. Critically, one can observe how these parameters impact future behaviors and social interactions, thus making it possible to observe the *evolution* of both the cognitive process and the cultural phenomenon in general. A good validated model can be used (and tested) to predict behaviors in different scenarios.

## Limitations

RL models have been fruitful in explaining various individual and social phenomena. The underlying idea is that complex behaviors are implemented by seemingly simpler cognitive functions such as learning, memory, and attention. However, two major limitations should be noted: (1) This approach has difficulty integrating societal or macro-phenomena; and (2) critically, has not yet very successfully integrated linguistic aspects of behavior, which are very important for cultural transmission. We believe that these issues pose more as an opportunity because they will allow improvements and refinements for RL models as well as allow for integrating RL models with complimentary approaches.

## Conclusion: The Central Role of Uncertainty

Uncertainty is a dominant concept across all the phenomena we have examined in this chapter. Tight and loose cultures can be to some extent reduced to degrees of uncertainty over the space of available or probable actions. Environmental or social changes are materialized as a modification of the underlying distribution of expectations, as well as the connections between actions and outcomes. Cultural mixing and biculturalism increase the uncertainty of options, and therefore their success depends on the ability of the agents to either integrate different probability distributions or successfully switch between mental models and their associated probability distributions. Niche construction necessitates explorative actions, thus implying some tolerance to uncertainty and reliance on action selection rules such as the softmax principle.

Critically, both social and individual learning can be conceived of as a response to environmental uncertainty. Henrich and McElreath (2003) and Castro and Toro (2004) seem to agree that environmental variability influences individual and social learning. Individual learning is a suitable answer to quick environmental changes but may not be sufficient for successful interaction with strategic social and cultural agents. On the other hand, cultural learning implies the adoption and evaluation of learned action–outcome associations that have been successful for a long period of time but not long enough to be genetically transmitted (see Gintis, 2011).

Cognitive neuroscience has so far provided a very detailed computational account of how reinforcement and other forms of learning happen. Factors that might inhibit or enhance learning have been confidently established. On the other hand, culture neuroscience can enrich the learning literature by offering a broader view of the scope of learning. Computational Cultural Neuroscience could become a tool that elegantly explains individual and group responses to uncertainty, under a wider evolutionary and social viewpoint.

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# PART 2

# Cultural Neuroscience of Emotion

CHAPTER

6

# Cultural Values Modulate Emotional Processing in Human Amygdala

Tetsuya Iidaka *and* Tokiko Harada

## Abstract

This chapter reviews how cultural values modulate emotional processing in the amygdala? Here we discuss a functional magnetic resonance imaging experiment whereby Japanese participants performed an emotional dot-probe task in which they were presented with an unpleasant picture (insect) and a neutral picture (chair). The unpleasant picture condition evoked a greater amygdala response. Between-condition differences in amygdala response were negatively correlated with individualism and collectivism cultural value scores, indicating that individuals who were more collectivistic showed a greater amygdala response. In a second experiment, we modulated individual cultural differences (individualism vs. collectivism) with a cultural priming task in Japanese participants, half of whom were primed with an individualistic scenario and half with a collectivistic scenario. Significant activation of the right amygdala was observed in the collectivistic-primed group. Biological variability in responses to emotional stimuli exists in individuals living in a relatively unitary culture, such as Japan; the neural response of the amygdala was significantly associated with the cultural values of individualism and collectivism.

**Key Words:** fMRI, self-construal, priming, attention, anxiety, culture

## Introduction

Arguments persist about whether the variety of human emotion is determined biologically or culturally, and whether emotion is universal or culture-specific. Cross-cultural similarities and differences in emotion have been identified in various aspects of emotional processing involving perception, appraisal, physiological reaction, behavior, and regulation (Mesquita & Frijda, 1992). Indeed, previous research has shown that cross-cultural similarities in one aspect of emotion do not necessarily imply similarities in other aspects; despite the universality of central nervous system responses, components such as facial expressions, voice intonations, and regulation and generation of emotional behavior may differ between cultures. Moreover, the particular aspects chosen for investigation have important implications for questions of cross-cultural differences and similarities. Thus, in this chapter, we regarded the neural response in the amygdala, as measured by functional magnetic resonance imaging (fMRI), as a critical component of emotional response in the human brain.

The amygdala is a subcortical structure that plays a critical role in motivated and emotional behavior, and it is specialized for evaluating and responding to cues that signal social and environmental threats (Adolphs, 2002; Phelps & LeDoux, 2005). Bilateral damage to the human amygdala severely impairs the ability to recognize emotions from facial expressions, as well as the capacity to make social judgments based on facial expressions (Adolphs, Tranel, & Damasio, 1998; Adolphs, Tranel, Damasio, & Damasio, 1994). Recent neuroimaging studies have demonstrated a significant activation of the human amygdala during tasks involving not only emotional faces (Fusar-Poli et al., 2009) but also scenes and objects with negative emotional valence (Sabatinelli et al., 2011). For instance, amygdalar activity elicited by the presentation of disgusting stimuli, such as an image of a cockroach, was significantly correlated with a self-rated scale of disgust sensitivity (Stark et al., 2005). In the domain of psychopathology, a review examined studies of amygdalar activation due to fear- or anxiety-related stimuli on presenting to patients with specific phobias; the findings suggested a linear relationship between subjective experience of negative affect and amygdala activation (Del Casale et al., 2012).

Studies employing both neuroimaging and genetic methodologies have found that a variety of genes impact amygdala responsiveness to anxiety-related stimuli. These genetic variants consist of genes that had been previously believed to be associated with anxiety disorder (e.g., the serotonin transporter gene polymorphism (5-HTTLPR), catechol-*O*-methyltransferase, monoamine oxidase A, and brain-derived neurotrophic factor (BDNF)). Furthermore, anxiety-related dimensional traits such as phobia proneness, harm avoidance, trait anxiety, behavioral inhibition, introversion, and negative bias were associated with limbic activation, including the amygdala's involvement in processing emotional stimuli. Imaging genetic studies of anxiety-related traits and anxiety disorders suggest that genetic alterations in serotonergic, dopaminergic, neuropeptides, and BDNF-related neurotransmission mediate emotional processing in the fear circuit involving the amygdala (Domschke & Dannlowski, 2010).

Furthermore, recent advances in our understanding of cultural differences in brain activity associated with emotional processing revealed that amygdalar responses could be modulated by culture and ethnicity. In an fMRI study using fearful and non-fearful faces in two distinct cultures (i.e., native Japanese in Japan and Caucasians in the United States), researchers found greater amygdalar activation in response to fearful faces expressed by members of participants' own cultural group (Chiao et al., 2008). In another study that used only Caucasian faces and both Asian and Caucasian participants, Asian participants exhibited a stronger amygdalar response, particularly in response to the presentation of angry male Caucasian faces (Derntl et al., 2012). These results indicate substantial cultural effects—specifically, of participant background and experimental stimulus—on amygdalar activity. However, the means by which culture might affect neural responses to stimuli other than facial expressions have not been investigated.

It has been argued that the way in which people define themselves and their relations with others is a fundamental process in which cultural values shape cognitions. In particular, two self-construal styles (SCSs) have been identified across cultures and ethnicities: individualism and collectivism (Markus & Kitayama, 1991; Oyserman & Lee, 2008). Those who endorse individualistic (IND) values view people as independent of each other and describe individuals by using stable personality traits, whereas those who endorse collectivistic (COL) values view people as being highly interconnected. In addition, people have demonstrated continuous degrees of individualism and collectivism, as measured by the SCS questionnaire. SCSs have a significant influence on emotions and behavior (Cross, Hardin, & Gercek-Swing, 2011), with studies suggesting that IND traits are associated with decreases in depression (Okazaki, 1997; Sato & McCann, 1998), general anxiety (Hardin, Varghese, Tran, & Carlson, 2006; Kim, Kasser, & Lee, 2003; Xie, Leong, & Feng, 2008), and social anxiety (Hardin et al., 2006; Hong & Woody, 2007; Okazaki, 1997; Xie et al., 2008). Therefore, while considering a biological link between the amygdala and anxiety, we hypothesized that IND traits would be associated with less amygdalar activity; COL traits, meanwhile, would be associated with greater activity in response to emotionally negative stimuli.

The effects of SCS on neural responses have previously been investigated using fMRI and a self-judgment task (Chiao et al., 2009); however, the way in which SCS affects emotional processing and amygdalar response, in particular, has never been studied. We aimed to elucidate the relationship between the amygdala, cultural values, and emotion by presenting anxiety-related objects to the participants while measuring neural responses. The amygdalar activity elicited by disgusting objects was correlated with participants' SCS. Moreover, behavioral studies have demonstrated that people can readily acquire cultural schemas, and several different cultural primes have elicited either individualistic or collectivistic orientations within the individual (Oyserman & Lee, 2008). However, to date, the ways in which cultural priming might affect the amygdalar response to emotional stimuli have not been investigated. The second aim of this study, therefore, was to test whether amygdalar activity in response to disgusting stimuli could be altered by this culture priming procedure.

In the current study, we investigated whether the amygdalar responses to objects with negative emotional valence might be related to participants' SCS, using fMRI and an emotional dot-probe task with native Japanese individuals living in Japan. In this task, originally developed by Posner and colleagues (Posner, Snyder, & Davidson, 1980), two words, faces, or pictures that varied in emotional salience (e.g., threat vs. neutral) were simultaneously presented in different locations (e.g., left vs. right) to the participants, after which a neutral object (the probe) appeared in the location previously occupied by one of two stimuli. Participants were instructed to press a response button immediately upon perceiving the probe, and their reaction time (RT) was recorded. Based on previous studies (e.g., Posner, Snyder, & Davidson, 1980), we predicted that participants would detect probes that appeared in the location of the emotional stimuli faster than those that appeared in the location of the neutral stimuli.

This RT effect is thought to be caused by the participants' attentional bias to emotional stimuli; indeed, participants with a high anxiety level showed more attentional bias to the emotional stimuli in previous research (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van IJzendoorn, 2007; Frewen, Dozois, Joanisse, & Neufeld, 2008; MacLeod, Mathews, & Tata, 1986). The RT may be faster when the probe appears in the location of the threat because individuals with a high anxiety level pay more attention to threat stimuli. In the other condition, wherein the probe appears in the location of the neutral stimulus, the RT may be slower because of the additional time required to shift attention from the threat stimuli to the neutral stimuli. In previous fMRI experiments that used the emotional dot-probe task, significant differences in amygdalar activity were observed between these conditions (Britton et al., 2013; Carlson, Reinke, & Habib, 2009; Monk et al., 2004).

In our first experiment, we hypothesized that greater activation of the amygdala would be observed in the condition wherein the probe was shown on the same side as the negative stimuli (pictures of insects) compared to the condition in which the probe was shown on the same side as the neutral stimuli (pictures of chairs). Furthermore, we predicted that SCS score would be linked to amygdalar activity. In our second experiment, we manipulated participant SCS, employing cultural prime to shift the SCS to either an IND or a COL orientation. These primes included reading a story about a warrior whose selection was based on either merit or familial relations, or thinking for a short time about what makes one unique or similar to one's friends and family (Chiao, Harada, et al., 2010; Oyserman & Lee, 2008; Trafimow, Triandis, & Goto, 1991). We assessed whether such priming—toward either an IND or a COL orientation—modulated amygdalar response, as measured by fMRI during the emotional dot-probe task.

## Experiment 1

### *Method*

#### PARTICIPANTS

The participants of Experiment 1 were 17 right-handed healthy adults, all of whom were native Japanese individuals living in Japan (11 men and 6 women; mean age, 22.5 years; standard deviation (SD)= 3.0 years) and had normal or corrected-to-normal vision. Written informed consent was obtained from each participant prior to the experiment. The study was approved by the ethics committee of the National Institute for Physiological Sciences and Nagoya University School of Medicine.

#### SELF-CONSTRUAL SCALE

We defined individualism and collectivism based on the participants' self-report on the Self-Construal Scale (Singelis, 1994). First, to calculate each participant's SCS index, the mean agreement for the 12 individualistic and 12 collectivistic items in the Self-Construal Scale was calculated for each participant. Each participant's SCS index was then calculated using a simple scoring algorithm [SCS index = the mean agreement for the IND items – the mean agreement for the COL items]. Then, we used the participants' SCS indices as a continuous variable to conduct a correlational analysis to explore the strength of the relationship between SCS and neural activity during the task.

#### STIMULI

Digitized color pictures of 24 insects and 24 chairs, obtained from the Internet, were used as stimuli (Figure 6.1). The insect pictures included a spider, a cockroach, a fly, and a moth, all of which are considered to be disgusting in Japanese culture. Adobe Photoshop (Adobe Systems Incorporated, San Jose, CA) was used to standardize the size (206 × 206 pixels) of all of the photographs and to apply a gray background to all of them. The stimuli were projected onto a transparent screen hung on the bore of a magnet approximately 65 cm from the

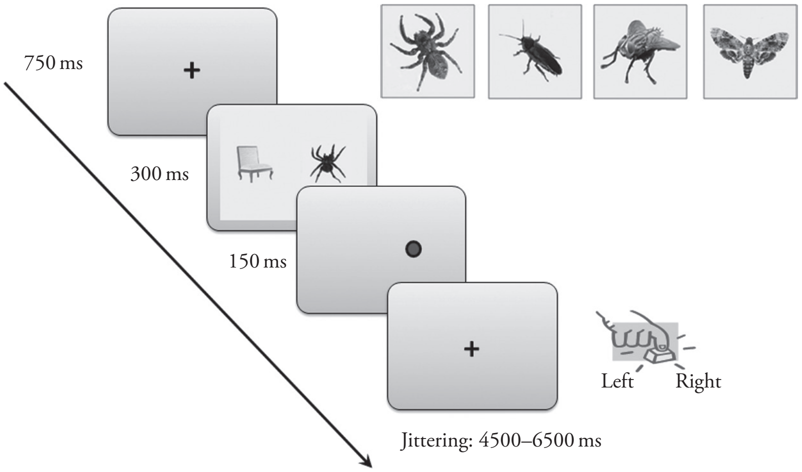

**Figure 6.1** The experimental procedure and an example of the stimuli that were used After the fixation point (duration = 750 ms), pictures of insects and chairs were shown side-by-side on the screen for 300 ms; then, a blue dot appeared on the right or left side of the center of the screen for 150 ms. The participants determined on which side the blue dot appeared and pressed either the right or the left button of the response box as fast and accurately as possible. The intertrial interval was jittered between 4500 and 6500 ms. Four kinds of insects (i.e., a spider, cockroach, fly, and moth) are shown in the right upper.

participants' eyes. The participants viewed the stimuli through a tilted mirror attached to a head coil.

### EXPERIMENTAL PROCEDURE

The participants were scanned while they performed an emotional dot-probe task (Figure 6.1). The experiment consisted of three event-related functional runs, with 48 trials each. Each trial began with the presentation of a fixation point for 750 ms, followed by stimulus pictures, which were presented for 300 ms, and then a blue dot, which was presented for 150 ms. A picture of an insect was paired with a picture of a chair, and these were shown side-by-side on the center of the screen. There were 48 distinct pairs of insect and chair images, and the insect and chair images were presented with an equal frequency on the left and right side of the screen. The blue dot was shown randomly on either the left or the right side of the screen. A stimulus picture and a blue dot occupied approximately 7.6° and 0.8° of visual angle, respectively. Trials were separated by a blank screen, which was presented in a jittered manner, with the duration ranging from 4500 to 6500 ms (average intertrial interval, 5500 ms).

For each trial, the participants made a judgment about which side of the screen (left side or right side) the blue dot appeared, and they pressed either the left or the right button of the response box held in their right hand as accurately and fast as possible. We hypothesized that the insect pictures would induce negative emotion and draw participants' attention more as compared to the chair pictures; therefore, we predicted that the participants would respond faster when the dot was presented on the insect side than when it was presented on the chair side. The order of stimuli was randomized within and between the runs. The stimuli were presented and participant's responses were recorded by using Presentation (Neurobehavioral Systems, Albany, CA).

After the scanning, the participants rated their impression of the insect pictures, which had been shown in the emotional dot-probe task, on a 4-point Likert scale (1 = neutral, 2 = somewhat awful, 3 = moderately awful, and 4 = extremely awful), outside the scanner room. Each picture was shown on the computer screen for 300 ms followed by a fixation period, which lasted for 3000 ms, and the participants were instructed to rate them by pressing 1, 2, 3, or 4 on the keyboard before the fixation point disappeared from the screen. Finally, the participants completed the Self-Construal Scale (Singelis, 1994).

### fMRI DATA ACQUISITION

The functional brain images were acquired at the National Institute for Physiological Sciences in Okazaki, Japan. Scanning was conducted on a 3.0-T Siemens Allegra MRI scanner equipped with single-shot, echo-planar image (repetition time = 2000 ms; echo time = 30 ms; flip angle = 75°; field of view = 192 mm, 64 × 64 matrix; 26 slices; voxel size = 3 × 3 × 4 mm), sensitive to blood oxygen level-dependent contrast.

After discarding the first four images, which were affected by nonuniformity of the magnetic field, the remaining 165 successive images in each run were subjected to analysis. The accuracy and RT of the response were measured and statistically analyzed using a paired *t*-test (significance threshold of 0.05).

### fMRI DATA ANALYSIS

Data were analyzed using SPM8 software (Wellcome Department of Imaging Neuroscience, London) implemented in MATLAB (MathWorks, Natick, MA). First, all volumes were spatially realigned to the mean volume, and the signal in each slice was realigned temporally to that obtained in the middle slice, using sinc interpolation. The resliced volumes were normalized to the Montreal Neurological Institute (MNI) space by using an echo-planar imaging template of SPM8. The normalized images were spatially smoothed with an 8-mm Gaussian kernel. After preprocessing, the statistical analysis for each individual subject was conducted using general linear modeling. At the first level, each single event was modeled as a hemodynamic response function at the onset of the response. The six parameters of the participant's head movement during the scan were also included as regressors in the model. High-pass frequency filters (cutoff = 128 s) and an autoregressive (AR (1)) model were applied to the time series data for each participant. For each participant, the two conditions (i.e., responses to a dot shown on the same side as an insect image (insect condition) and those shown on the same side as the chair image (chair condition)) were modeled separately. The contrast images containing brain responses for the insect condition, the chair condition, and the difference between the insect and chair conditions were created. These contrast images were statistically analyzed by the second-level one-sample *t*-tests. The significance threshold was set at $p = 0.001$, uncorrected, and $k = 10$ voxels.

To explore the relationship between the brain responses and SCS, a simple regression analysis was conducted using the contrast images between the insect and chair conditions and the SCS index. The region of correlation analysis was restricted within the spherical region of interest (ROI) with a 10-mm radius centered at the right amygdala peak voxel ($x, y, z = 26, 0, –22$) as defined by the subtraction analysis between the insect and chair conditions. The signal extracted from the right amygdala peak voxel was correlated with the SCS index across the 17 subjects (Pearson's correlation coefficient, significance threshold = 0.05).

## *Results*

### SELF-CONSTRUAL SCALE

The means (SDs) of the IND and the COL scores across the 17 participants were 4.70 (0.53) and 4.75 (0.57), respectively. The mean of the SCS index (i.e., the IND score – the COL score) was –0.04 (SD = 0.70; range, –2.0 to 1.2).

### BEHAVIORAL DATA

There was no significant difference in mean accuracy between the insect and chair conditions (99.3% and 99.6%, n.s.). As predicted, the mean RT for the insect condition was significantly lower than the mean RT for the chair condition (insect, 356 ms (48 ms); chair, 362 ms (49 ms); $p = 0.03$; one-tailed paired *t*-test). The mean rating of the insects (2.8 (0.6)) was significantly worse than the mean rating of the chairs (1.0 (0.1) ($t = 11.6$; $p < 0.01$; one-tailed paired *t*-test).

### fMRI SUBTRACTION AND CORRELATIONAL ANALYSES

The one-sample *t*-tests revealed that the right amygdala and adjacent regions were more active in the insect condition than in the chair condition (Figure 6.2). Several other regions in the entorhinal cortex and ventral striatum had a greater response for the insect condition than the chair condition (Table 6.1). On the other hand, there was a greater response in the superior frontal gyrus for the chair condition than for the insect condition (Table 6.1). A simple regression analysis revealed a significant negative correlation between right amygdalar activity and the SCS index (Figure 6.3A, arrow; $x, y, z = 26, –8, –16$; $Z = 3.90$; $p = 0.001$; uncorrected; $k = 11$ voxels). The signal extracted from the peak voxel and the SCS index was plotted in Figure 6.3B. There was a significant negative correlation between these values ($r = –0.82$, $p < 0.01$). When the two subjects who were the most individualistic and the most collectivistic were excluded from the analysis, there was still a significant negative correlation between the amygdalar activity and the SCS index ($r = –0.60$, $p < 0.05$). Thus, the participants with higher collectivistic traits showed greater amygdalar activity when the insect image and the dot were shown on the same side.

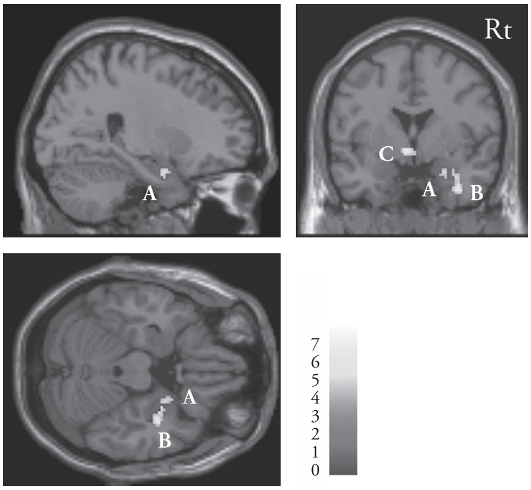

**Figure 6.2** A significant activation in the subtraction analysis between the insect and chair conditions is superimposed on a canonical template of SPM8. The threshold was set at $p = 0.001$, uncorrected, and $k = 10$ voxels. The detailed information of the cluster is shown in Table 6.1. A, right amygdala; B, right entorhinal cortex; C, ventral striatum.

## Experiment 2

### *Method*

#### PARTICIPANTS

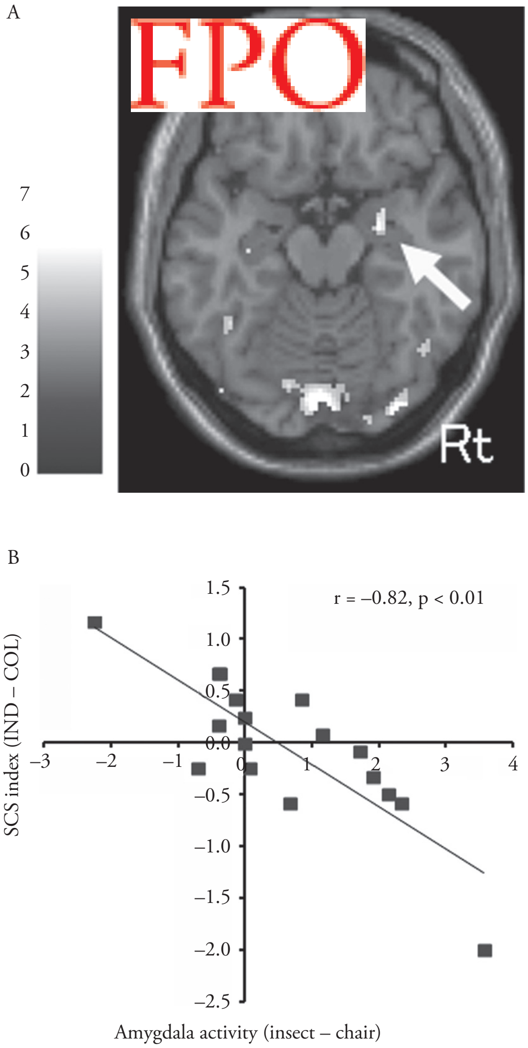

**Figure 6.3** (A) The results of whole brain regression analysis revealed a significant and negative correlation between the SCS index and amygdalar activity (white arrow). (B) The correlational result is plotted in the figure. The vertical axis indicates the SCS index (IND – COL), and the horizontal axis indicates amygdalar activity (insect – chair). A regression line, a Pearson's correlation coefficient, and the $p$ value are shown.

The participants of Experiment 2 were 20 right-handed healthy people, all of whom were native Japanese living in Japan. All had normal or corrected-to-normal vision, and all had not participated in Experiment 1. Ten participants (7 men and 3 women; mean age, 19.7 years; SD = 0.9 years) were assigned to the individualistic prime (IND-PRIME) group, and the remaining 10 participants were assigned to the collectivistic prime (COL-PRIME) group (6 men and 4 women; mean age, 22.4 years; SD = 3.9 years). Written informed consent was obtained from each participant prior to the experiment. The study was approved by the ethics committee of the National Institute for Physiological Sciences and Nagoya University School of Medicine.

**Table 6.1. Results of Subtraction Analysis Between the Insect and Chair Conditions in Experiment 1**

| Region (BA) | Laterality | *x, y, z* | Voxels | *Z* value |
|---|---|---|---|---|
| **Insect – chair** | | | | |
| Entorhinal cortex (36) | Rt | 36, –4, –26 | 211 | 4.80 |
| Amygdala[a] | Rt | 26, 0, –22 | | 3.47 |
| Ventral striatum | Lt | –4, 2, –6 | 149 | 4.53 |
| Entorhinal cortex (36) | Lt | –34, –8, –32 | 27 | 3.48 |
| **Chair – insect** | | | | |
| Superior frontal gyrus (8) | Lt | –16, 28, 52 | 66 | 4.10 |

[a] Entorhinal cortex and amygdala in the right hemisphere are in a single cluster.

[b] The threshold at $p = 0.001$, uncorrected, and $k = 10$ voxels.

BA, Brodmann's area; Rt/Lt, right/left hemisphere.

### PRIMING PROCEDURE FOR THE INDIVIDUALISTIC AND COLLECTIVISTIC GROUPS

In a room outside the scanner, the participants completed a 10-min priming procedure comprising two priming tasks: the Japanese version of the Sumerian Warrior Story (SWS) task (Trafimow et al., 1991) and a modified version of the Similarities and Differences with Family and Friends (SDFF) task (Trafimow et al., 1991). Both of these have been previously shown to reliably affect self-concept (Chiao, Harada, et al., 2010; Oyserman & Lee, 2008; Trafimow et al., 1991). In the Japanese version of the SWS, the participants read a story describing a dilemma in which Samurai, a military general, is deciding which warrior to send to a Shogun. In the IND-PRIME condition, the participants read a version of the story in which Samurai chooses a warrior who is the best qualified for the job. In the COL-PRIME condition, the participants read a version of the story in which Samurai chooses a warrior who is a member of his family. After reading the story, all participants judged whether they admired the general by circling one of three responses (yes, no, or not sure) to the question, "Do you admire Samurai?" Next, the participants completed a modified version of the SDFF priming procedure. In the IND-PRIME condition, the participants were asked to think about what makes them different from their family and friends and then to write a short essay about what they expect themselves to do. In the COL-PRIME condition, participants were asked to think about what they have in common with their family and friends and then to write a short essay about what their family and friends expect them to do.

### THE SELF-CONSTRUAL SCALE QUESTIONNAIRE

As in Experiment 1, the SCS (Singelis, 1994) was used in Experiment 2 to define the participants' individualism and collectivism. Each participant's SCS index was calculated as described for Experiment 1.

### STIMULI

The stimuli for Experiment 2 were the same as those used for Experiment 1.

### EXPERIMENTAL PROCEDURE

After the priming procedure, participants were scanned while performing the emotional dot-probe task (Figure 6.1). The behavioral data were statistically analyzed by conducting the two-way analysis of variance (ANOVA) with group (IND-PRIME and COL-PRIME) and condition (insect and chair) as factors. The significance threshold was set at 0.05.

### fMRI DATA ACQUISITION

The functional brain images were acquired in exactly the same manner as that describe for Experiment 1. The accuracy and RT of responses were measured and statistically analyzed by conducting two-way ANOVA with group (IND-PRIME and COL-PRIME) and condition (insect and chair) as factors (threshold of $p = 0.05$).

### fMRI DATA ANALYSIS

The image data obtained for the IND-PRIME and COL-PRIME groups were analyzed in exactly the same way as described for Experiment 1. The contrast images for the difference between the insect and chair conditions were statistically analyzed using a one-sample $t$-test for each group. A two-sample $t$-test between the groups was conducted with age and sex of the participants included as covariates. The significance threshold was set at 0.005, uncorrected, and $k = 5$ voxels. In this analysis, we report here only the clusters within the medial temporal lobe including the amygdala, the hippocampus, and the parahippocampal gyrus.

## *Results*

### PRIMING PROCEDURE

For the IND-PRIME group, the participants' responses to the Japanese version of the SWS task were as follows: yes, 8; no, 1; not sure, 1 (the numerical value indicates the number of participant responses). For the COL-PRIME group, the participants' responses to the Japanese version of the SWS task were as follows: yes, 3: no, 3; not sure, 4 (the numerical value indicates the number of participants).

### BEHAVIORAL DATA

The mean of the SCS index in the IND-PRIME and COL-PRIME groups was 0.11 (1.07) and –0.19 (0.91), respectively. There was no significant difference in the SCS index between the priming groups (one-way ANOVA, $F$ (1, 18) = 0.45, $p$ = 0.51). The behavioral data obtained during the fMRI experiment are shown in Table 6.2. Although there was no significant main effect or interaction effect involving group (IND-PRIME vs. COL-PRIME) in accuracy and RT, the mean RT was significantly lower for the insect condition than the chair condition (two-way ANOVA, $F$ (1,

**Table 6.2. Behavioral Results of Experiment 2**

| | IND-PRIME | COL-PRIME |
|---|---|---|
| **Accuracy (%)** | | |
| Insect | 98.3 (2.2) | 98.3 (3.2) |
| Chair | 98.5 (2.6) | 98.8 (2.0) |
| **Reaction time (ms)** | | |
| Insect[a] | 391 (93) | 351 (58) |
| Chair | 401 (102) | 360 (53) |
| **Post-scan rating** | | |
| Insect[b] | 3.1 (0.7) | 3.3 (0.4) |
| Chair | 1.1 (0.2) | 1.0 (0) |

[a] The mean RT was significantly ($p < 0.01$) faster for insect condition than for chair condition.

[b] The mean post-scan rating was significantly ($p < 0.05$) worse for insect than for chair.

18) = 10.2, $p < 0.01$). In the post-scan rating, the insect was rated significantly worse than the chair ($F$ (1, 18) = 250, $p < 0.01$), with no significant group difference detected ($F$ (1, 18) = 0.28, $p = 0.59$).

### fMRI DATA ANALYSIS IN EACH GROUP AND BETWEEN GROUPS

In the COL-PRIME group, there was significant activation of the right amygdala (*x, y, z* = 26, –6, –20; $Z = 3.15$; $k = 49$ voxels) in the subtraction analysis between the insect and chair conditions (Figure 6.4A, left). The cluster survived at $p = 0.05$ after applying a small volume correction within a spherical ROI with an 8-mm radius centered at the peak amygdala voxel. On the other hand, there was no such activation in the region of medial temporal lobe including the amygdala and hippocampus for the IND-PRIME group even at a lenient threshold of $p = 0.05$, uncorrected (Figure 6.4A, right). The mean signal extracted from the right amygdala (*x, y, z* = 26, –6, –20) across the participants of the COL- and IND-PRIME groups is shown in Figure 6.4B. The results of a two-sample *t*-test between the groups with age and sex as covariates showed that there was significantly greater activation in the regions of the left amygdala, right hippocampus, and left parahippocampal gyrus of the COL-PRIME group (Figure 6.5). The detailed information of these clusters is shown in Table 6.3.

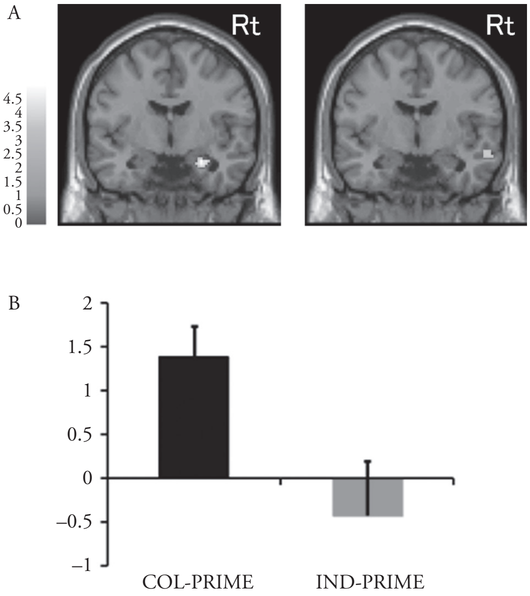

**Figure 6.4** (A) Left: The results of the subtraction analysis between the insect and chair condition in the COL-PRIME group are shown (*y* = –6 mm). There was a significant activation of the right amygdala (*x, y, z* = 26, –6, –20) at the threshold of $p = 0.005$, uncorrected, and $k = 49$ voxels. Right: The results of the subtraction analysis between the insect and chair condition in the IND-PRIME group are shown (*y* = –6 mm). There was no activation of the amygdala at a lenient threshold of $p = 0.05$, uncorrected, $k = 5$ voxels. (B) The mean and one standard error of signal extracted from the right amygdala (*x, y, z* = 26, –6, –20) are shown for the COL- and the IND-PRIME group.

## Discussion

The current fMRI study investigated the relationship between SCS and amygdalar activity in two separate experiments. In Experiment 1, the activity of the right amygdala, involved in the attentional bias to the negative emotional stimuli, was significantly and negatively correlated with the participants' individualistic and collectivistic traits. Thus, as collectivistic traits increased, so did amygdalar activity. In the second experiment, the participants' cultural values were modulated by priming tasks toward an individualistic or a collectivistic orientation. We observed significant amygdalar activation in response to the negative stimuli in the collectivistic-primed group but not in the individualistic-primed group. These results suggest that participants' SCS had a cultural effect on emotional processing in the amygdala; furthermore, these findings imply that an individual's cultural values are dynamic and can be modulated by priming. We note that the Japanese participants

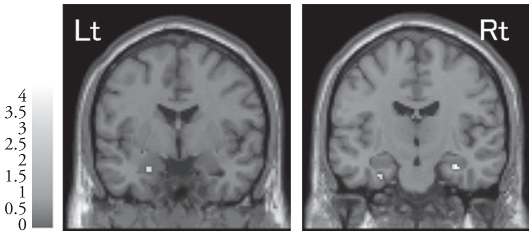

**Figure 6.5** The results of the two-sample *t* test between the COL- and IND-PRIME groups are shown in a canonical template of SPM8 (left, at $y = -2$ mm; right, at $y = -14$ mm). There were significant differences in the activation of medial temporal lobe brain structures, including the left amygdala (left), the left parahippocampal gyrus (right), and the right hippocampus (right). The detailed information of these clusters is shown in Table 6.3.

in the study exhibited a large amount of variability in their SCS index scores; this tendency had emerged in previous studies using the SCS questionnaire (Elliott & Coker, 2008; Hardin et al., 2006; Hong & Woody, 2007; Okazaki, 1997; Sato & McCann, 1998). This lack of uniformity suggests that individual differences within a society are a major factor regulating physiological responses of the brain associated with emotional processing. The distinction on the IND/COL dimension is therefore unlikely to be a fixed disparity that characterizes certain cultures; rather, it may be flexible in relation to the particular circumstances of the individual.

The use of the dot-probe task in fMRI experiments has revealed the neural correlates of attentional bias to emotional stimuli in the fields of cognitive (Armony & Dolan, 2002; Carlson et al., 2009; Fani et al., 2013; Monk et al., 2004) and developmental (Britton et al., 2013; Lindstrom et al., 2009) neuroscience and clinical psychiatry (Amico et al., 2012; Fani et al., 2012). However, to date, only three studies have shown a significant relationship between the task and amygdalar activation (Britton et al., 2013; Carlson et al., 2009; Monk et al., 2004). In a study by Monk and colleagues (2004), masked angry and neutral faces were presented to the participants. Researchers observed increased activation of the right amygdala when the condition in which the probe was presented on the side opposite to the angry face was compared with the condition in which the angry face and the probe were presented on the same side (Monk et al., 2004). In the second study, a backward masked fearful face presented in the left visual field enhanced attention to the target dot and increased neural activation in the left amygdala (Carlson et al., 2009). In the third study, amygdalar activity was greater in the condition in which the threat and probe were on opposite sides rather than in the condition in which they were on the same side (Britton et al., 2013).

In two of these studies (Britton et al., 2013; Monk et al., 2004), the results were contrary to those observed in the current study with regard to the congruency of stimuli–probe location. However, in the research conducted by Britton and colleagues, there was no significant behavioral attentional bias to the threat face. In the study conducted by Monk and colleagues, attentional bias was away from threat stimuli because the RT was high when the stimuli and probe were presented on the same side; the results were indicative of low anxiety-level participants (Bar-Haim et al., 2007; Frewen et al., 2008). Therefore, the current study is the first to demonstrate a significant involvement of the human amygdala in the attentional bias to negative emotional stimuli associated with a faster response to a congruent, rather than an incongruent, condition using the emotional dot-probe task.

In a behavioral study that investigated the relationship between SCS and scores of self-report measures of depression and social anxiety, researchers found a significant negative correlation between the individualistic trait and social anxiety (Okazaki,

**Table 6.3 The Results of Two-Sample *t*-test Between COL-PRIME and IND-PRIME Groups in Experiment 2**

| Region (BA) | Laterality | *x, y, z* | Voxels | *Z* value |
|---|---|---|---|---|
| Hippocampus | Rt | 32, –14, –22 | 16 | 3.35 |
| Amygdala | Lt | –24, –2, –24 | 6 | 2.75 |
| Parahippocampal gyrus (36) | Lt | –24, –10, –32 | 12 | 2.92 |

[a] The threshold at $p = 0.005$, uncorrected, and $k = 5$ voxels.
[b] The significant results are restricted in the region of medial temporal lobe, including amygdala, hippocampus, and parahippocampal gyrus.
BA, Brodmann's area; Rt/Lt, right/left hemisphere.

1997) and a positive correlation between the collectivistic trait and depression (Sato & McCann, 1998). A relative individualistic to collectivistic score of the SCS correlated positively with a happiness rating and negatively with an anxiety rating (Kim et al., 2003). Two other studies showed that individualistic traits were negatively associated with anxiety scores (Hong & Woody, 2007; Xie et al., 2008). Overall, these behavioral observations have shown that emotional symptoms such as depression, unhappiness, and anxiety can be influenced by SCS, and the individualistic trait tends to decrease negative and increase positive affect. These notions fit with the current study's results, which showed a negative correlation between the SCS index and amygdalar activity due to the neural response being induced by attentional bias to negative stimuli.

It has been reported that self-construal priming procedures effectively modulate human behavior and its neural correlates as measured by fMRI. In a study that used a face judgment task of one's own face as well as those of familiar persons, researchers found a greater activation of the right prefrontal cortex in response to own-face presentation after independent self-construal priming (Sui & Han, 2007). In another study that investigated self-related neural activity in the medial prefrontal cortex, individualistic priming increased activity in these brain regions during general self-judgment, whereas collectivistic priming increased brain activity during contextual self-judgment (Chiao, Harada, et al., 2010). Finally, collectivistic and individualistic priming modulated resting state activity in the default mode network in the medial prefrontal and posterior cingulate cortices (Wang, Oyserman, Liu, Li, & Han, 2013). These studies demonstrated that cultural priming changed the degree of neural activation in brain regions involved in a given task to a culturally expected orientation. Thus, to our knowledge, the current study is the first to reveal changes in amygdalar activity in response to emotional stimuli in the context of collectivistic and individualistic cultural priming.

What is the neural mechanism underlying reduced amygdalar activation after the individualistic priming that we observed in the current study? The results most likely reflect enhanced evaluation and integration of culturally congruent set representation. It has been suggested that priming of collectivism or individualism temporarily orients individuals to attend to or shift attention from negative emotional stimuli. These emotional processing biases could affect amygdalar activity because individualistic traits are linked to less anxiety compared to collectivistic traits. In addition, in recent fMRI research using volitional regulation of emotion during the processing of fearful pictures, willful effort to detach subject from emotional responses reduced heightened amygdalar activity (Schardt et al., 2010). Specifically, this effect was observed in the subjects with short alleles of the 5-HTTLPR gene, which is associated with anxiety traits. Because more than 90% of Japanese subjects have such genes (Murakami et al., 1999), top-down inhibitory mechanisms from the prefrontal cortices may have been active during the cultural priming task in the current study. Interestingly, there was a significant reduction in the activation of the default mode network during the resting state after individualistic priming (Wang et al., 2013). Thus, during an fMRI experiment, individualistic priming affects positive and task-related activity and negative and task-unrelated activity. Although we used an event-related design with a short interval (~5.5 s) in our experiment, cultural priming may have modulated the baseline activity between the stimuli and the events.

However, we note that the current fMRI observations may only hold true for Japanese participants because collectivistic values and anxiety may be tightly coupled in their native culture; the link between the two variables may result in strong amygdalar activation. Therefore, future studies using participants from individualistic cultural groups are necessary to elucidate how SCS modulates emotional behavior and its neural underpinnings. The finding of a greater priming effect for individualistic values on amygdalar activity may be limited to participants from Asian cultures, in which people are highly interconnected.

Several fMRI studies have shown that the culture and ethnicity of the participants and experimental stimuli affected amygdalar activity in response to human faces (Chiao et al., 2008; Derntl et al., 2012; Greer, Vendemia, & Stancil, 2012; Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005; Rule et al., 2010). The results, however, are inconsistent. For example, in a study using both Black and White American participants and neutral face pictures, researchers found significantly greater amygdalar activation in response to a Black American face in both groups of participants (Lieberman et al., 2005). In another study that used Caucasian and Japanese participants and pictures of facial expressions from these two cultures, there was greater amygdalar activity in response to fearful faces of their own culture compared with those of a different culture (Chiao et al., 2008). In contrast, both American and Japanese participants exhibited greater amygdalar activation in response to faces of politicians who were members of another cultural group (Rule et al., 2010). These results, despite some important inconsistencies, imply that culture and ethnicity may affect amygdalar responses to facial stimuli—both of one's own and of other group members—in multifaceted ways.

In addition, the complexity of a participant's experience with a given culture and social environment may have a substantial influence on neural activity. For example, the amygdalar response to White American faces was significantly and positively correlated with the scores of previous exposures to race-related incidents for Black American participants (Greer et al., 2012). In a sample of Korean individuals living in Europe, researchers found that the shorter their duration of stay, the stronger the amygdala response to the presentation of Caucasian faces (Derntl et al., 2012). Thus, neural plasticity involving social and cultural experiences may modulate human behavior and brain responses.

In cross-cultural comparisons of psychiatric symptoms, adolescents in the United Kingdom reported higher levels of anxiety than adolescents in Japan (Essau et al., 2011). Epidemiological studies assessing the 12-month prevalence of social anxiety disorder (SAD) showed that the rate was nine times higher in the United States than in Japan (7.1% vs. 0.8%) (Hofmann, Anu Asnaani, & Hinton, 2010); however, culture-specific presentations of anxiety disorder in Japan, namely *Taijin Kyofusho* (TKS), may not have been included in the results. TKS has frequently been discussed as a cultural-specific expression of SAD that is believed to be particularly prevalent in Japanese and Korean cultures. Similar to individuals with SAD, individual with TKS are concerned about being observed and consequently avoid a variety of social situations. Nevertheless, the presence and severity of TKS may not be appropriately evaluated by using standard diagnostic criteria and questionnaires developed in Western cultures. In addition, the 12-month prevalence of major depressive episodes in all age groups is approximately four times higher in the United States than in Japan (8.3% vs. 2.2%) (Kessler et al., 2010), although the suicide rate in Japan is more than double that in the United States (24.2 vs. 11.0 per 100,000, 2005 data; http://www.who.int/mental_health/prevention/en). This suggests that preclinical subjects with depressive and anxiety symptoms, who do not receive appropriate treatment by mental health experts, are more common in Japan than in the United States.

Finally, in terms of stimulus and scanner validation, our experimental methods have several advantages compared to those used in other studies (Chiao, Hariri, et al., 2010). Prior research suggests that people feel stronger emotions when they encounter culturally specific stimuli; however, a validated set of emotional stimuli to be used with different ethnicities does not yet exist. Unfortunately, this presents a serious methodological limitation to cultural neuroscience research. Hence, the results of the current experiments, in which a single cultural group and culturally appropriate stimuli were used, may provide significant and robust findings with regard to the neural underpinnings of emotion–culture interactions. Furthermore, to date, there is no established method to account for the possibility of variability in fMRI performance across different scanner facilities. Therefore, the results of studies that used different scanners in different institutes may have been confounded by factors such as differences in scan protocols, baseline signal variation, and signal-to-noise ratios. The use of one scanner per study, as in our protocol, can eliminate all of these potential confounds.

## Conclusions

The current study demonstrated, using fMRI and an emotional dot-probe task, that the cultural dimension of individualism versus collectivism may reliably affect emotional processing at a neural level. Through two independent studies with samples of native Japanese participants, we discovered that collectivistic traits tend to produce increased activity in the human amygdala—a critical brain structure involved in negative emotional processing. We speculate that for people living in collectivistic cultures such as Japan, heightened attention and an increased amygdalar response to negative information may be advantageous to achieving collectivistic cultural norms. According to such norms, the maintenance of social harmony is highly valued and people are required to be more attentive to the perspectives of others (Chiao & Blizinsky, 2010). For example, a greater vigilance to negative information may be useful for the early detection of another person's expression of anger or fear, and it could help avoid actions or interpersonal situations that may induce negative emotional states in others.

Western individuals high on the IND trait are encouraged to influence others by changing others' behavior to meet their needs, whereas Eastern individuals high on the COL trait are encouraged to adjust by changing their own behavior in line with others' needs. In Western culture, in which a high-arousal emotional state is valued, influence is more salient; in Eastern culture, however, in which a low-arousal emotional state is valued, adjustment is more salient (Tsai, Miao, Seppala, Fung, & Yeung, 2007). With respect to the relationship between influence/adjustment and SCS, Japanese participants who demonstrated high scores on the COL trait tended to perceive the emotional stimuli as highly salient compared to those who scored high on the IND trait. Therefore, participants with high COL trait scores and who were primed by the COL scenario were more likely to show enhanced responses in the amygdala than those who had high IND scores and were primed by IND scenario.

Studying the relationship between the amygdala, culture, and emotion may help us understand the bio-socio-psychological underpinnings of mental disorders, such as anxiety disorder and major depression. These conditions have been biologically characterized by heightened amygdalar activity, reduced prefrontal inhibitory mechanisms, and malfunctions of the interactions between these brain regions. Cross-cultural epidemiological studies have shown that there are substantial differences in the prevalence rate of the disorders; however, the diagnostic procedures that were developed in one culture may not be appropriate in others. Nevertheless, measuring amygdala activity using fMRI proposes a potential biomarker for diagnosing and preventing such disorders and for evaluating responses to drug and cognitive therapies.

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## CHAPTER 7

# Genes, Brain, and Culture Through a 5-HTT Lens

Michio Nomura

## Abstract

How do genes affect the human brain, cognition, and culture? This chapter focuses on these interrelated areas through the lens of the serotonin transporter (5-HTT), specifically examining the behavioral regulation system in Japanese people. First, relationships between the 5-HTT gene and impulsive behavior under aversive conditions are discussed. Next, this chapter shows that in collectivistic nations, individuals with higher interdependent self-construal optimize activation of the right ventrolateral prefrontal cortex (rVLPFC) when suppressing thoughts of death. Finally, as a function of psychosocial resources, higher levels of social trust affect adaptive processes and increase rVLPFC activity, all of which are geared toward modulating social pain. Thus, S allele carriers are more likely to adapt to collectivistic cultures because of the functional properties of the S allele, which may in turn promote collectivistic cultural norms.

**Key Words:** serotonin, 5-HTT gene, prefrontal cortex, impulsivity, general trust, interdependent self-construal, Japanese population

## Introduction

How do genes affect the human brain, cognition, and culture? Psychological and neuroimaging studies with concurrent biochemical or pharmacological measurements of serotonin (5-hydroxytryptamine, 5-HT) function, especially those investigating the effect of gene polymorphisms, are useful in clarifying the relationships between social cognition and culture.

This chapter focuses on these interrelated areas through the lens of the serotonin transporter (5-HTT), specifically examining behavioral regulation in the Japanese population. Serotonin has a wide range of biological effects on human, nonhuman primate, and rodent behaviors, and dysfunctional 5-HT transmission in the central nervous system may contribute to behavioral disorders characterized by impulsivity (LeMarquand, Benkelfat, Pihl, Palmour, & Young, 1999; Nomura et al., 2006; Walderhaug et al., 2002). 5-HT has also been shown to modulate the impact of punishment-related signals on learning, with aversive emotionality promoting response inhibition (Cools, Roberts, & Robbins, 2008).

## 5-HTT Gene Variations in Different Cultures

A number of studies have shown that compared to the long (L) allele of the 5-HTTLPR gene *SLC6A4*, the short (S) allele, which is a major variant in Japan (Kumakiri et al., 1999), leads to excess 5-HT in the synaptic cleft due to lower concentrations of 5-HTT mRNA and less 5-HT reuptake (Canli & Lesch, 2007; Lesch et al., 1996). The biochemical mechanism associated with the 5-HTTLPR S allele is thought to result in enhanced neural processing of aversive environmental cues and greater amygdala activation during presentation of fearful faces, which could be related to an attentional bias for negative stimuli (Beevers, Gibb, McGeary, & Miller, 2007; Osinsky et al., 2008) and an increased risk of neuroticism, anxiety (Kaufman et al., 2004), and emotional regulation disorders in the context of early and adult life adversity (Caspi et al., 2003).

Population genetics research has revealed that approximately 80% of the Japanese population carries the S allele polymorphism, whereas only 40% of Europeans carry this allele (Gelernter, Kranzler, & Cubells, 1997; Kumakiri et al., 1999). It is worth considering the cultural implications of the relationship between 5-HTTLPR gene prevalence and environmental factors. For example, individualistic cultures encourage people to consider themselves as independent from each other, whereas collectivistic cultures endorse the idea that people are highly interconnected to one another and favor the maintenance of social harmony over the assertion of individuality (Kitayama & Cohen, 2007; Markus & Kitayama, 1991; Nisbett, Peng, Choi, & Norenzayan, 2001;). Studies on population genetics imply that the population frequency of S allele carriers and the population frequency distribution of cultural collectivism are matched: Greater population frequencies of S allele carriers are associated with increases in cultural collectivism (Chiao & Blizinsky, 2010). Japan is considered to be a collectivistic culture.

Why then does genetic selection exist for the S relative to L allele carriers in Japan? What are the underlying mechanisms? In the following sections, I discuss data that are relevant to this issue, with reference to our study on the association between the S allele and impulsivity (Nomura et al., 2015).

## Psychological and Biological Mechanisms of Impulsivity

### *Serotonin and Impulsivity*

In order to evaluate motor impulsivity in an aversive context, we adopted the reinforcement punishment–reward task (Go/NoGo; LeMarquand et al., 1998, 1999). To match the population prevalence in Japan (Kumakiri et al., 1999; Mizuno et al., 2006), we compared ss versus sl carriers, who were grouped in previous studies as S carriers, to ll carriers (e.g., Caspi et al., 2003). Of the 61 participants (34 men; mean age, 29.0 ± 1.1 years (mean ± SE)), 26 carried the sl genotype, and 34 carried the ss genotype. In this study, we were careful to match subjects for both sex and education (years).

The reinforcement punishment–reward Go/NoGo task uses punishments or rewards to promote response activations or suppressions. In the task, participants were required to press a computer key when a "Go" stimulus appeared on a screen (randomly assigned numbers) but to withhold this response when a "NoGo" stimulus appeared (other randomly assigned numbers). Only one stimulus was presented at a time, and the participants learned the process through trial and error. Dependent measures for this task included errors of commission (Go responses to NoGo stimuli), with a larger number of commission errors indicating greater difficulty in inhibiting impulsive behavior.

The Go/NoGo task was assessed using four different conditions, the order of which differed across participants. Under the reward-only (RR: Rew-Rew) condition, participants were rewarded for both responding to the Go stimuli and withholding responses to the NoGo stimuli. Under the punishment–reward (PR: Pun-Rew) condition, participants were punished for withholding responses to the Go stimuli while being rewarded for withholding responses to the NoGo stimuli. Both these conditions were considered "reward NoGo conditions" because participants were rewarded when they withheld responses to a NoGo stimulus. Under the punishment-only (PP: Pun-Pun) condition, participants were punished when they withheld responses to the Go stimuli and responded to the NoGo stimuli. Under the reward–punishment (RP: Rew-Pun) condition, participants were rewarded for responding to the Go stimuli but punished for responding to the NoGo stimuli (Figure 7.1). The conditions consisted of two sessions, in accordance with the task procedure

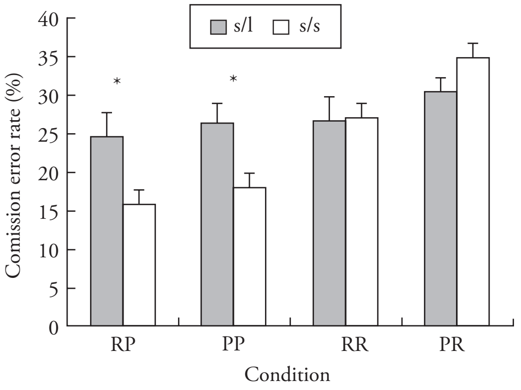

**Figure 7.1** Response–outcome contingencies in the experimental conditions. In the "reward NoGo conditions," participants were rewarded when they withheld responses to the "NoGo" stimuli: Under the reward-only (RR) condition, participants were rewarded for responding to the "Go" stimuli; under the punishment–reward (PR) condition, participants were punished for withholding responses to the "Go" stimuli. PP, punishment-only; RP, reward–punishment. The level of significance for correlation is denoted by *$p < .05$.

reported by LeMarquand et al. (1998): Each stimulus was presented on the screen for 800 ms, with a 1300-ms inter-trial interval. Rewards were given for a correct response and were denoted by a 10¢ monetary feedback. Punishments were classified a wrong response and were denoted by a 10¢ deduction from the participant's earnings.

### *5-HTT Gene Affects Impulsivity Under Aversive Contexts*

We found that compared to subjects in the sl group, those in the ss group made fewer impulsive responses, specifically under aversive conditions for committing such errors, without showing any effects on overall motor inhibition ($p < .05$; Figure 7.1). A one-way analysis of variance of omission errors revealed no significant main effects or interactions, indicating that 5-HTT gene polymorphisms had no effect on omission errors. Furthermore, no statistical differences were observed for reaction times for hits and commission errors. What is most interesting is that aversive feedback specifically affected impulsive responses of the ss group but not those of the sl group. These findings were robust after controlling for group differences in age, education, and gender. These results suggest that polymorphisms in the 5-HTT gene do not directly affect the behavioral regulatory process itself but may instead exert effects via the mechanism for evaluation of potential risk.

### *Role of the 5-HTT Gene in Maintaining Cultural Norms*

As mentioned previously, compared to Americans, Japanese tend to have negative reactions toward norm violations and support sanctioning of violators (Gelfand, Nishii, Chan, Yamaguchi, & Triandis, 1998). The Japanese society is an example of a "tight" society (Chan, Gelfand, Triandis, & Tzeng, 1996; Pelto, 1968; Triandis, 2004) in which severe sanctions are imposed on those who deviate from social norms. This social tendency seems to be consistent with our biological data, suggesting that the relatively effective regulation of behavior in response to punishment associated with the S allele may play a major role in the maintenance of social order in Japanese society. Because maintaining social order is important in tight societies, S allele carriers are more likely to adapt to such cultures because of the functional properties of the S allele, which might in turn promote collectivistic cultural norms (Fredrickson, 2001; Isen, Daubman, & Nowicki, 1987).

### *Association Between 5-HTT and Risk for Depression and Anxiety*

One could argue that if the S allele is a risk factor for depression and anxiety (Caspi et al., 2003; Kaufman et al., 2004), Japanese people should be vulnerable to emotional disorders. However, the reality appears to be the opposite, as suggested by epidemiology studies showing a lower prevalence of DSM-IV (*Diagnostic and Statistical Manual of Mental Disorders*, fourth edition; American Psychiatric Association, 1994) mental disorders, such as anxiety and depression, in Japan compared to Western populations (Kawakami et al., 2005; Weissman et al., 1996). Chiao and Blizinsky (2010) reviewed studies in cultural psychology that examined self-construal across cultures, focusing on individualism and collectivism. Their research showed that increased cultural collectivism, which is associated with a greater population frequency of S allele carriers for the 5-HTT gene, is associated with a decreased prevalence of anxiety and mood disorders. Thus, one possible explanation for the greater prevalence of S allele carriers in Japan may relate to adaptation to collectivistic cultural norms via genetic selection. Our next question was to examine why an increased cultural collectivism corresponds with a decreased prevalence of anxiety and mood disorders by examining the underlying brain mechanisms.

## Role of Culture and Personality Traits in Brain Functions

### *Psychosocial Resources Decrease the Impact of Social Pain*

Social exclusion evokes social pain, which can trigger various interpersonal difficulties such as impulsivity, aggression, and depression. Recent studies suggest that people with ample psychosocial resources experience fewer negative effects during or after social exclusion (Eisenberger, Taylor, Gable, Hilmert, & Lieberman, 2007; Kross, Egner, Ochsner, Hirsch, & Downey, 2007). Such resources can include interpersonal assets, intrapersonal attributes, belief systems, and transitory affective states (Cohen, Aronson, & Steele, 2000; Harber, Einev-Cohen, & Lang, 2008; Scheier & Carver, 1985; Seligman, 1975).

General trust, a specific type of trust, has been considered to be a valuable social resource (Putnam, 2000). According to the emancipation theory of trust (Yamagishi, Cook, & Watabe, 1998), general levels of trust may determine how people respond to interpersonal events. This theory proposes that people with high general trust are often able to expand their social networks, whereas people with low general trust prefer to rely on assured networks of established relationships (Yamagishi, 1998).

All of these resources can reinforce people against adversity and promote adaptive responses to challenges. Compared to individuals with few psychosocial resources, people with greater psychosocial resources may experience diminished social pain responses because they have a higher threat-detection threshold, meaning that events are less likely to be perceived as threatening in terms of social exclusion, and/or they are more effective at regulating the threat once detected. Neuroimaging studies suggest that this social pain is associated with activation of the dorsal anterior cingulate cortex (dACC), with its further regulation being reflected by activation of the right ventrolateral prefrontal cortex (rVLPFC).

The rVLPFC is involved in cognitive control of attention, emotions, and impulses and in regulation of social pain evoked because of social exclusion (Eisenberger, Lieberman, & Williams, 2003; Hariri, Bookheimer, & Mazziotta, 2000). In addition, compared to people with high rejection sensitivity, those with low rejection sensitivity more often show high levels of rVLPFC activation during a social exclusion task (Kross et al., 2007). Unsurprisingly, the VLPFC is one of the brain areas that play a primary role in adaptation to the environment. Therefore, we used near-infrared spectroscopy (NIRS) to examine whether the increase in VLPFC activity related to general trust during social exclusion helps to buffer against social pain.

### *General Trust Moderates Social Pain by Activating the Prefrontal Cortex*

We conducted this study in 40 healthy Japanese undergraduates (27 women; mean age, 19.1 years) and performed NIRS while they played an online ball-tossing game in which they were socially rejected. The participants saw a ball, two other players on the left and right sides of the screen, and an arm representing the participant on the lower center portion of the screen. The other players threw the ball to each other or to the participant. Under the inclusion condition, participants received six or seven throws per block. The participant could return the ball to one of the players by pressing one of two keys. Under the social exclusion condition, participants received just one or two throws (from task onset to 10 s into the task). After this point, the other two players completely stopped throwing the ball to the participant for the remainder of the scan. Following each condition, participants completed a questionnaire that assessed social pain to determine the subjective experiences of participants. Responses were along the lines of "I felt liked" or the reverse items, "I felt rejected," "I felt invisible," and "I felt I was unable to influence the actions of others."

Behavioral results showed that levels of general trust correlated negatively with self-reported social pain following exclusion ($\beta = -.32$, $p < .05$). Furthermore, general trust correlated positively with rVLPFC activity, although no such relationship with self-esteem was seen.

We assigned participants to high or low general trust groups based on their general trust scores (high, $n = 17$; low, $n = 20$) and then compared temporal rVLPFC activation between these two groups. Individuals in the high general trust group exhibited greater changes in oxygenated hemoglobin levels than those in the low general trust group when social exclusion began ($t(35) = -3.03$; $p < .01$; Figure 7.2).

Based on interrelationships among the level of general trust, neural activity in the rVLPFC, and self-reported social pain, we sought to determine whether activity in the rVLPFC mediates the relationship between general trust level and self-reported social pain. Results based on multiple regression modeling revealed that the rVLPFC mediated the direct path from general trust to self-reported social pain (Sobel test, $z = -1.96$, $p < .05$). After controlling for activation of the rVLPFC, the path from

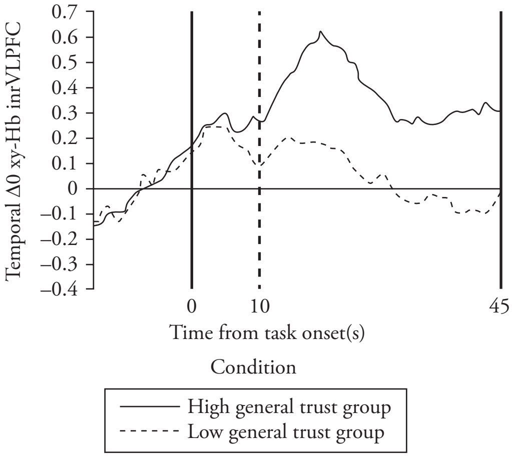

**Figure 7.2** Temporal changes in oxygenated hemoglobin levels (Δoxy-Hb) in the right ventrolateral prefrontal cortex (rVLPFC) during the social exclusion conditions. Group means for the high general trust and low general trust groups are shown. ESE = explicit social exclusion.

Source: Yanagisawa et al. (2011).

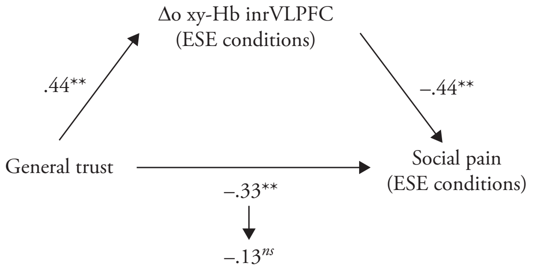

**Figure 7.3** A mediation model tested whether rVLPFC activity (Δoxy-Hb in rVLPFC) explained the association between general trust and social pain during social exclusion conditions. The level of significance for correlations are denoted by $^{*}p < .05$ and $^{**}p < .01$.

Source: Yanagisawa et al. (2011).

general trust to self-reported social pain was no longer significant (β = −.13, *p* = .43; Figure 7.3).

Taken together, these findings suggest that general trust probably affects the course of a series of adaptive processes, all of which are geared toward the modulation of social pain. General trust, a specific type of trust, has been considered to be a valuable social resource. Social exclusion would be expected to induce feelings related to the loss of relationships for excluded individuals (Smart Richman & Leary, 2009). The current findings suggest that general trust serves to buffer against such feelings. Studies have yet to examine whether general trust affects interpersonal behavior after social exclusion. However, if indeed general trust regulates social pain, people with high general trust would be expected to differ from those with low general trust in terms of interpersonal behavior subsequent to social exclusion.

Next, we examined whether individual differences in interdependence self-construal in Japan, a collectivist dimension, are related to the VLPFC activity.

### *Interdependent Self-Construal Alleviates the Fear of Death*

Because neuroimaging results converge to suggest that rVLPFC activity functions to suppress threats (Nomura, Ohira, Haneda, Iidaka, Sadato, Okada, et al., 2004; Ochsner & Gross, 2005), we examined whether individual differences in personality—specifically interdependence self-construal—are related to rVLPFC activity when the subject is primed with cues related to the concept of "death" versus "negative."

Thirty undergraduates (17 women; mean age, 19.85 ± 1.26 years) participated in this study. Participants first completed a word relationship task in which the negative condition used *kanji*, or Chinese characters, either taken from the plant category, such as "tree" and "flower," or related to negative concepts, such as "damage" and "grief." The death condition used words either drawn from the plant category or related to death, such as "coffin." The second task involved evaluating two essays (with 7-point scales) for "positive" and "negative" concepts. Participants read each essay and evaluated the writer, using 14 items such as "How much do you like this person?"

The results showed that regardless of essay type, people with higher levels of interdependence gave higher essay scores to writers presenting concepts of death (β = −.38, *p* < .001). These results suggest that people with higher interdependence self-construal evaluated essay writers more positively when they were presented with death-related concepts rather than negative concepts (Figure 7.4).

Interestingly, people with higher interdependence showed increased rVLPFC activity during exposure to death-related information but not during exposure to negative information (β = .22, *p* < .05). However, no such relationships were found for lVLPFC activity, suggesting that interdependence

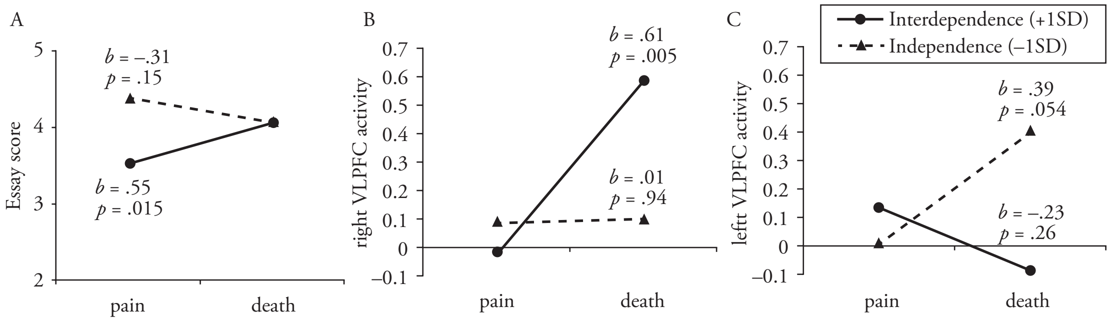

**Figure 7.4** Regression analysis predicting (A) essay score, (B) rVLPFC activity, and (C) lVLPFC activity from cultural self-construal scores for each condition (death vs. pain). Predicted regression values are plotted 1 standard deviation above and below the mean.

self-construal may affect inhibitory neural activity, manifesting as a suppression process against reminders of death (Figure 7.4). Results based on multiple regression modeling revealed that the rVLPFC mediated the direct path from condition to essay score (Sobel test, $z = 2.08$, $p < .05$). Mediation analysis showed that after controlling for rVLPFC activity, the path from condition to essay score was no longer significant in the interdependence-dominant group ($\beta = .002$, $p = .99$), suggesting that rVLPFC mediated the direct path from condition to essay score.

These findings suggest that interdependent self-construal may facilitate rVLPFC activity, which is implicated in suppressing fear of death and thereby influencing positive interpretations of death-related information.

The current study used NIRS to measure prefrontal cortex activity; therefore, we could not investigate possible correlations between activity in deeper brain structures and social exclusion conditions or general trust.

## Future Questions

Considering that the current findings were observed in a Japanese population, it would be interesting to determine whether 5-HTTLPR variability or rVLPFC activity has a similar effect in Western societies.

It is also of interest to determine the differences within similar geographic regions. For example, in Asia, because more than 80% of Koreans are collectivistic, whereas only approximately 50% of Japanese are collectivistic, which is much closer to the prevalence of Western societies (Chiao & Blizinsky, 2010), cultural differences might be responsible for such inconsistencies. Thus, our findings need to be replicated across other populations using the same variants.

## Conclusion

The main points of this chapter were first to question whether genetic selection exists for S relative to L allele carriers in Japan. We found that S allele carriers are more likely to adapt to collectivistic cultures because of the functional properties of the S allele, which might in turn promote collectivistic cultural norms.

Our second question asked why increased cultural collectivism corresponds with a decreased prevalence of anxiety and mood disorders. In collectivistic nations, individuals with higher interdependent self-construal optimize activation of the rVLPFC in the process of suppression specific to the fear of death, and thus tend to interpret subsequent information more positively. Furthermore, rVLPFC appears critical for regulating social pain.

In addition, as psychosocial resources, general trust impacts on a series of adaptive processes and increases rVLPFC activity, which are all geared toward modulating social pain.

Since Japan was devastated by an earthquake and tsunami in 2011, the Japanese police have reported receiving thousands of missing wallets containing approximately $48 million in cash. When faced with such a disaster and running short of life's necessities, such as food and money, due to the uncertainty of the situation, one would most likely be motivated to secure oneself, one's family, and one's friends. However, the people who returned valuables likely did so to individuals they had never met. One could suppose that these people are ethical and in control of their impulses. However, at the same time, because the Japanese provide an example of a "tight" society in which severe sanctions are imposed on individuals who deviate from social norms, it is not just a simple cliché to say that the Japanese are an ethical people. I also stress that based on the behavioral and biological data presented here, general trust and collectivism are important factors leading to such ethical behaviors.

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CHAPTER

# 8

# Embodied Brains, Social Minds: Toward a Cultural Neuroscience of Social Emotion

Mary Helen Immordino-Yang

**Abstract**

Psychologically, the emotions we feel about ourselves and about other people, known as social emotions, shape the very essence of our acculturated selves, including our relationships, morality, beliefs, and decisions. Neurobiologically, these emotions co-opt neurobiological mechanisms whose original, evolutionary purpose is to feel and regulate the body and to manage homeostasis. This confluence of social psychological and biological homeostatic functions has important implications for our understanding of human development, culture, and learning. Understanding the dynamic interplay of biology and culture in emotion will require integrating perspectives from anthropology, cultural psychology, psychiatry, child development, social affective neuroscience, and other disciplines, but it will ultimately shed new light on the inherently social nature of the human mind. Progress in this direction is reviewed, including experimental evidence, theoretical insights, practical benefits, and challenges.

**Key Words:** embodiment, social learning, emotion, culture, education, neuroscience

## Introduction: Why a Cultural Neuroscience of Social Affective Processing?

Anyone involved in raising and educating children knows that social learning is a major force in children's development. Typical children watch and engage with other people, imitate these other people's behaviors (including mental behaviors and beliefs), and look to trusted adults and peers for emotional and other feedback on their own behavior and beliefs (Harris, 2012). They imagine how other people feel and think, and those thoughts in turn influence how they feel and think. In this way, as anthropologists, cultural psychologists, and developmental psychologists have long described, children's social experiences, which are inherently culturally organized, influence how they come to think, act, and perceive the world (Bronfenbrenner & Bronfenbrenner, 2009) and shape individuals into acculturated adults.

This social perspective on human development, in my view, provides one central impetus for the foundation of a new research field in the cultural neuroscience. Because the brain develops in accordance with the demands placed on it (Greenough, Black, & Wallace, 1987; Nithianantharajah & Hannan, 2006), over time, cultural biases in how individuals act, think, and feel in the social world are likely to influence both the neural processing that undergirds individuals' developing mental abilities and the development of brain structures and connectivity. Understanding the nature of these influences would provide an unprecedented source of information about natural biological and social variation among human beings. Specifically, it would enrich neuroscientific models of psychological processing by helping to elucidate the aspects of our current understanding that may be culture specific, and it would enrich psychological models by helping to clarify the neurobiological mechanisms underlying mind-level differences. For example, it would give insight into whether two cultural groups who display different behavior are actually accomplishing this behavior differently at the level of the brain, and conversely whether two groups who display similar behavior may actually be recruiting different neural mechanisms (Immordino-Yang, 2013). To date, socially related variability in brain development has been studied almost exclusively in relation to deprivation, either due to socioeconomic factors or due to abuse/neglect (e.g., Cicchetti, 2004; Farah et al., 2008; Stevens, Lauinger, & Neville, 2009). In essence, bringing a cultural perspective into the study of affective and social neuroscience introduces an adaptive source of systematic variability in social norms and values into functional and structural brain data, allowing researchers to probe the normative influences of the social world on the social brain and vice versa (Immordino-Yang, 2010).

One important domain in which mutual influences between biological and cultural factors are likely to play out is social emotion. Social emotions, such as admiration, compassion, gratitude, indignation, or contempt, are the emotions individuals feel about other people or about inherently social constructs such as social situations, systems, and values. Social emotions can also extend to the emotions individuals feel about themselves as a social being, such as self-related compassion, inspiration, or frustration, and in these contexts can relate to identity and to what cognitive neuroscientists have termed "self-processing" (Banfield, Wyland, Macrae, Munte, & Heatherton, 2004; Northoff & Bermpohl, 2004).

New evidence from social and affective neuroscience is shedding light on the neural underpinnings of human social emotions, which range from basic, relatively automatic responses such as empathic reactions to another's physical pain or fearful reactions to an outgroup member's face (Chiao et al., 2008; De Vignemont & Singer, 2006; Olsson, Ebert, Banaji, & Phelps, 2005) to complex responses to others' mental states, such as admiration for another's virtuous accomplishments in the face of difficult obstacles or compassion for another's psychological pain in the face of loss or exclusion (Decety & Chaminade, 2003; Immordino-Yang, McColl, Damasio, & Damasio, 2009). Importantly, whereas basic, automatic responses to here-and-now social stimuli serve as a critical entry point into sociality, complex emotions such as admiration for virtue, gratitude, and compassion move the responder beyond the here-and-now to consider the broader picture of a person's quality of mind, given a cumulative set of social circumstances and inferences about that person's perspective, beliefs, and motives (Immordino-Yang, 2010). As such, these emotions play important roles in interpersonal relationships, motivation, and morality (Damasio, 2005), as well as in the construction of self and identity. They push individuals to emulate those whom they admire, help those for whom they feel compassion, shun those for whom they have contempt, and so on, and they motivate individuals to try to better themselves by acting in accordance with a broader system of societal values (Algoe & Haidt, 2009; Haidt, 2003; Keltner & Haidt, 1999; Schindler, Zink, Windrich, & Menninghaus, 2013).

Neurobiologically, we are learning that social emotions recruit neural systems related to high-level cognition and abstract thought, including neural processing related to social emotional experience and self (Haidt & Morris, 2009; Immordino-Yang et al., 2009), social cognitive processes such as perspective taking (Saxe & Wexler, 2005) and moral judgment (Casebeer & Churchland, 2003; Young, Cushman, Hauser, & Saxe, 2007), and social affective responses such as empathy and stereotype threat (Derks, Inzlicht, & Kang, 2008; Frith & Frith, 2007; Singer & Lamm, 2009). However, we have also learned that even the most cognitively complex versions of these emotions continue to build from basic mechanisms of pain, reward, and attachment and are "hooked" into neural mechanisms for basic biological survival (Damasio, 2012; Eisenberger & Lieberman, 2004; Panksepp, 2003). Even the most complex social emotions have been found to recruit basic neurobiological mechanisms for homeostatic regulation, visceral somatosensation, and consciousness, such as the brain stem, hypothalamus, and insula (Immordino-Yang et al., 2009).

From a social developmental perspective, taking the neural and psychological evidence together, these findings reveal that complex social emotional processing simultaneously motivates individuals to infuse their actions and decisions with moral perspectives and values and co-opts basic brain mechanisms for survival (Immordino-Yang & Sylvan, 2010). Because complex social emotional processing is shaped by cultural learning, it is entirely reasonable to conjecture that cultural practices organize and bias important aspects of brain function by reusing basic neural systems for social functions, potentially even systems related to basic physiological survival (Immordino-Yang, Chiao, & Fiske, 2010). To begin to appreciate what these may be, we turn now to an introduction to the neuroscience of social emotion.

## Embodied Brains, Social Minds

Traditional Western views of the mind and body, such as that of Descartes, divorced high-level, rational thought from what were thought of as the basal, emotional, instinctual processes of the body (Damasio, 1994/2005). By contrast, recent work in affective and social neuroscience has led to a new view of the mind. Far from divorcing emotions from thinking, this research collectively suggests that emotions, such as anger, fear, happiness, and sadness, are cognitive and physiological processes that involve both the body and the mind (Barrett, 2006; Damasio et al., 2000). As such, they utilize brain systems for body regulation (e.g., for blood pressure, heart rate, respiration, and digestion) and sensation (e.g., for physical pain or pleasure and for stomachache). They also involve and influence brain systems for cognition, changing thought in characteristic ways—from the desire to seek revenge in anger to the search for escape in fear, the receptive openness to others in happiness, and the ruminating on lost people or objects in sadness. In each case, the emotion results from a cognitive appraisal of a situation (Frijda, 1988) and then is played out on the face and body (Ekman & Friesen, 1975; Levenson, 1992). The physiological and postural changes to the face and body are then felt via neural somatosensory systems and are thought to form the basis of emotional feelings (Damasio & Carvalho, 2013). Also in each case, these feelings interact with other thoughts, often including semantic memories, episodic memories, and prospections (Immordino-Yang & Singh, 2013; Yang, Bossman, Schiffhauer, Jordan, & Immordino-Yang, 2013), to help people make sense of and learn from their experiences (Immordino-Yang & Damasio, 2007). Stated simply, affective neuroscience is revealing that the human mind is influenced by an interdependency of the body and brain. We should expect, therefore, that because culture influences the mind, it can credibly influence not only body physiology and behavior but also brain development and function. Understanding the dynamics of these dynamic influences will shed new light on human beings' inherently social biology and mind.

After all, cultural psychologists and anthropologists have long known that thinking and learning, as simultaneously cognitive and emotional processes, are not carried out in a vacuum but, rather, in social and cultural contexts (Fischer & Bidell, 2006; Vygotsky, 1978). Just as the mind is created by an embodied brain, an individual's mind is situated within a social context. A major part of how people think has to do with their past social experiences, reputation, and cultural history. During the past decade, social neuroscience has revealed some of the basic biological mechanisms by which social learning takes place (Frith & Frith, 2007; Mitchell, 2008; Tomasello, Carpenter, Call, Behne, & Moll, 2005). According to current theories, social processing and learning generally involve internalizing one's own subjective interpretations of other people's feelings and actions (Uddin, Iacoboni, Lange, & Keenan, 2007). We perceive and understand other people's feelings and actions in relation to our own beliefs and goals, and we vicariously try on these feelings and actions as if they were our own (Immordino-Yang, 2008). Just as affective neuroscientific evidence links our bodies and minds in processes of emotion, social neuroscientific evidence links our own selves, including our goal-directed actions (Lieberman, 2007), personal memories (Immordino-Yang & Singh, 2013), and empathic tendencies (Lieberman & Eisenberger, 2009), to the understanding of other people.

For example, how do we decide whether the Syrian government's use of chemical weapons against its own people in 2013 was wrong? Why do most people have such a difficult time understanding how a group of individuals were able to carry out such despicable actions? We automatically, albeit many times nonconsciously, imagine how the victims and perpetrators of these attacks must have felt and thought, empathically experiencing both what they were thinking about and their emotions around these thoughts. For many, just thinking of the media images of victims in the attack's aftermath empathically induces a fearful mindset with all its physiological manifestations, such as a racing heart and anxious thoughts. In the other direction, we have difficulty empathizing with the individuals who carried out the attacks because the values, morals, and emotions that motivated these individuals are so different from our own.

### *The Acculturated, Embodied Mind*

From the perspective of affective neuroscience, the social emotions that motivated these individuals to carry out the Syrian attacks, as well as the social emotions we experience when empathizing with the victims or trying to understand the perpetrators, represent a uniquely human achievement and one that is highly acculturated: the ability to feel emotions and engage in actions about the vicariously experienced beliefs of another person (Immordino-Yang, 2010). The ability to accomplish these complex emotional and moral deliberations likely involves the formation of increasingly complex and nuanced mental constructions around personal and cultural values, identity and self-awareness, and cognitive conceptualization of social situations, including through perspective taking and affective empathy. Social emotions and their associated thoughts and actions are biologically built but culturally shaped; they reflect our neuropsychological propensity to internalize the actions of others, but they are interpreted in light of our own social, emotional, and cognitive experiences. In other words, we act on our own accord but interpret and understand our choices by comparing them consciously or nonconsciously against the norms of our culture, learned through implicit and explicit social, emotional, and cognitive experiences as we subjectively perceived them (Immordino-Yang, 2011).

As is the case for basic emotions, the neural processes for experiencing and interpreting these various choices are not independent from our bodies or from homeostatic regulation of bodily physiology (Figure 8.1). Instead, social emotions, although arguably a pinnacle human achievement, remain biologically grounded in our most basic physiological life-regulatory processing (Decety & Chaminade, 2003; Immordino-Yang, McColl, Damasio, & Damasio, 2009). The feeling of these emotions appears to modulate the neural systems that sense stomachache (insula) and regulate blood chemistry (hypothalamus), for example. Especially intriguing, these emotions also involve systems associated with visceral self-awareness that are related to monitoring and regulating consciousness (e.g., the inferior posterior sectors of the posteromedial cortices, an ensemble of cortices in the middle of the back of the head composed of dorsal posterior and retrosplenial cingulate and inferior precuneus; Immordino-Yang et al., 2009). Quite literally, it appears that the ability to treat others as we would be treated, with all of the cultural bias that implies, relies on feeling the empathic welling in our throat or "punch" in our gut—feeling

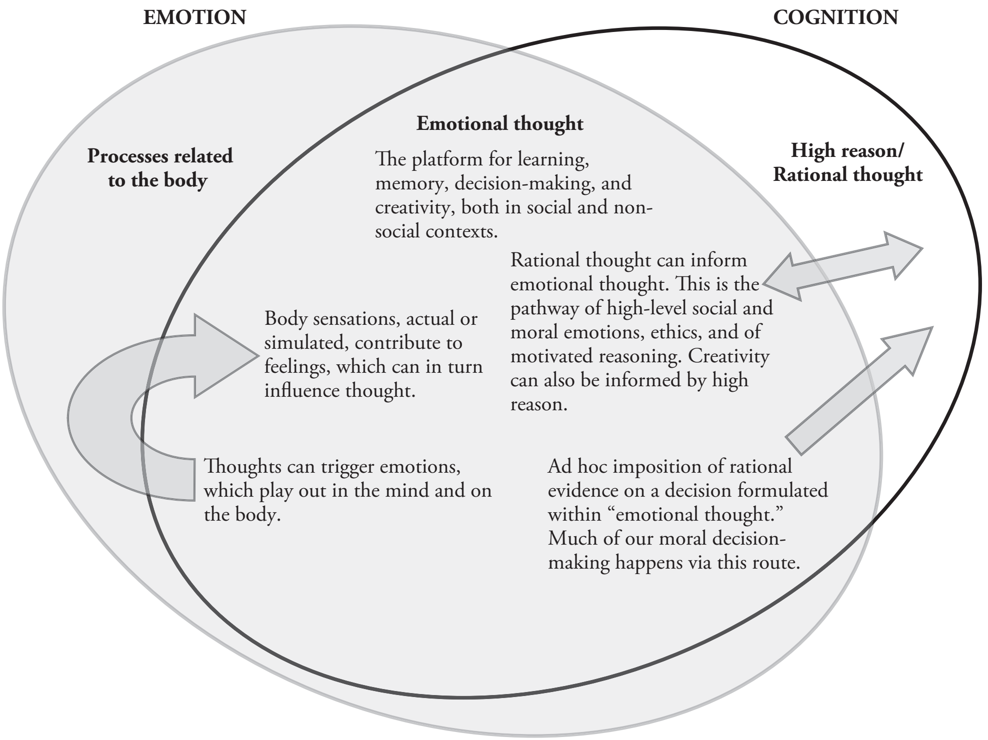

**Figure 8.1** Emotion and cognition come together to produce human thought processes. In the diagram, the solid ellipse represents emotion; the dashed ellipse represents cognition. The extensive overlap between the two ellipses represents the domain of "emotional thought." Culture likely shapes the development of emotional thought, in part through repeated revisiting of real or simulated bodily sensations in light of acquired social and moral values and cognition.

Source: Reprinted with permission from Immordino-Yang and Damasio (2007).

these on the substrate of our own psychological and bodily selves and interpreting them in light of personal experience and cultural knowledge—implicit and explicit, conscious and not. Understood from an interdisciplinary psychosocial and neurobiological perspective, the process of "feeling" social emotions, such as the moral indignation that swept the world in the wake of the Syrian attacks, involves integrating sociocultural models and knowledge with somatosensory information from bodily emotional expression (or mentally simulated expression that utilizes somatosensory neural mechanisms but does not seem to reflect real physiological activation of the body; Immordino-Yang, Yang, & Damasio, 2014) and interpreting these mental and bodily reactions in accordance with cultural expectations and values.

### *Evidence for Individual and Cultural Differences in Embodiment During the Experience of Social Emotion*

Cultural and individual differences in bodily arousal during social emotional processing have been well documented, and early evidence from cultural neuroscientific studies suggests that these differences may impact how individuals experience social encounters and feel accompanying social emotions. For example, East–West cultural differences in values related to emotion-related arousal and expressiveness (Tsai, 2007) have been found to relate to group-level differences in abilities to consciously perceive visceral sensations such as heartbeats, which in turn have been shown to predict individuals' reliance on visceral sensations versus the social context when sorting out one's reaction to an arousing social encounter (Ma-Kellams, Blascovich, & McCall, 2012). Other studies show that even among Westerners, individuals show substantial variability in sensitivity to embodied sensations (Critchley, 2004) and in the extent to which embodied sensations figure in conscious emotional experiences (Barrett, Quigley, Bliss-Moreau, & Aronson, 2004; Dunn et al., 2010); both of these measures have in turn been shown to co-vary with neural measures in somatosensory cortices, including with anatomical measures of cortical thickness (Craig, 2002) and with somatosensory activation during the experience of strong emotion (Saxbe, Yang, Borofsky, & Immordino-Yang, 2013). It is likely that some of this variability relates to learned modes of conceptualizing the feeling of embodied reactions during emotions (Barrett, 2006), a suggestion that holds implications for how interindividual variation in body sensation—a basic, automatic process—may translate into cultural differences in how complex emotions are processed and felt.

In an effort to explore the possibility that culture influences the social–emotional feeling process, in a series of experiments conducted in Beijing and Los Angeles, Immordino-Yang and colleagues engaged participants in a 2-h videotaped interview about a series of true, compelling social stories meant to induce varieties of admiration and compassion (Immordino-Yang et al., 2009; Immordino-Yang, Yang, & Damasio, 2014). The experimenter narrated each story and disclosed relevant information about the setting and circumstances, and then she showed each participant short videos depicting the story protagonist. She finished by prompting with the question, "How does this person's story make you feel?" or "你对这个人的故事有什么感受?" Following this interview, participants were moved to the functional magnetic resonance imaging (fMRI) scanner, where they saw the crux of each story they had discussed in the interview presented again in a shortened format, followed by a gray screen in which the participants were asked to reflect on the story and report the strength of their current emotional feeling. Blood oxygen level-dependent (BOLD) and psychophysiological data (electrocardiogram, respiration and galvanic skin response) were collected to measure participants' neural and heart-rate responses continually during the task.

Although all participants reported feeling strong emotions during the experiment and although there were no differences in the strength or frequency of reported emotions between the cultural groups, the researchers found differences in how participants from China and the United States discussed their feelings during the interview. This was not overly surprising, but the direction of difference was surprising: descriptions of embodied sensations during the interview were much more common and prominent among American participants. Even more intriguing, these differences corresponded to differences in the recruitment of somatosensory cortices during the experience of complex emotional feelings in the fMRI scanner, suggesting that differences in how individuals verbally explained their feelings were not simply convention or metaphor but, rather, corresponded to real neurobiological differences in how individuals processed emotion-related somatosensory brain activity (Immordino-Yang, 2013; Immordino-Yang et al., 2014; Saxbe, Yang, Borofsky and Immordino-Yang 2013). Whereas approximately two-thirds of American participants spontaneously mentioned embodied sensations in describing their feelings, none of the Chinese participants did, save one report of "goosebumps" (Immordino-Yang & Yang, 2013a).

For example, after hearing a story meant to induce compassion, one European American responded (as quoted in Immordino-Yang, 2013),

> I'm not very good at verbalizing emotions. But . . . um . . . I can almost feel the physical sensations. It's like there's a balloon or something just under my sternum, inflating and moving up and out. Which, I don't know, is my sign of something really touching.

Upon hearing the stories of individuals who remained dedicated to helping needy others despite difficult obstacles and personal sacrifices, meant to induce admiration for virtue, one African American woman responded (as quoted in Immordino-Yang, 2013),

> I notice the same thing like during . . . spiritual experiences. When I did used to attend church, like when I feel really close to God, like in the moment I feel the same charge, or something resonates with you a lot, or if you think something's beautiful or, you know . . . or if you are in awe of something . . . sort of like tingly? Maybe like the little hairs raise on your body.

By contrast, Chinese participants seemed to focus more on analyzing the implications of the situation in a less body-oriented, more direct and other-focused manner. For example, in responding to a compassion-inducing story about a young musician who is burned in a fire and can no longer live outside of the hospital, one young woman in Beijing explained (as quoted in Immordino-Yang, 2013),

> I think that all her expectations for the future are gone. The sudden loss makes her very disappointed, so she can't handle it. It's miserable. It's a pity. I feel bad for her.

As mentioned previously, individual and cultural differences in emotion-related speech corresponded to differences in the recruitment of somatosensory neural systems. The researchers found that in cortices that represent the musculoskeletal body in space (i.e., the arms and legs), such as superior lateral parietal regions, the American group showed activation when feeling emotions, whereas the Chinese group did not. In addition, among American participants, individual differences in affective language use during the interview predicted individual differences in activation of these same cortices during the subsequent fMRI scan, despite that individuals who used more affective language did not report feeling more strongly than individuals who used more cognitive language to describe their feelings (Saxbe et al., 2013).

In the anterior insula, a visceral interoceptive region also associated with processing emotional feelings and emotion awareness (Gu, Hof, Friston, & Fan, 2013), a more nuanced pattern emerged in the data. Although American and Chinese participants showed the same amount of activation during presentations of emotional stimuli and reported similar categories, strength, and frequency of emotional feelings, cultural group differences emerged in the trial-by-trial correlations between the neural activations and the participants' reported feelings. These differences were related to individual differences in participants' spontaneous emotional expressivity during the interview, and they persisted even after controlling for contributions of emotion-related cardiac arousal to the insula activation (Immordino-Yang et al., 2014).

The results suggest an intriguing and surprising conclusion: Cultural influences on how emotions are expressed in social situations may impact the neural process by which individuals become aware of and assess their feelings, even without impacting the overall strength of feelings that individuals experience. Perhaps these neural patterns reflect cultural values and practices related to emotional embodiment: The traditional East Asian (Confucian-derived) cultural emphasis on embodiment aims to calm and settle the body in order to engage in unbiased cognitive assessment of a social situation. By contrast, mainstream American culture assimilates the feeling of body reactions to "intuited" psychological information about one's "true" emotional reaction. For example, in one socioemotional competence curriculum widely used in United States schools, children are expressly taught to attend to their embodied sensations as a way to recognize and manage their emotions adaptively (Brackett, Rivers, Reyes, & Salovey, 2012; Brackett, Rivers, Shiffman, Lerner, & Salovey, 2006). Current work is investigating these possibilities by examining how more in-depth, ethnographic interviews about individuals' experiences, personality, and cultural history may contribute to explaining these patterns (Immordino-Yang, 2013); how these patterns may emerge across child and adolescent development; and how they may be related to individuals' biological predispositions, such as to vagal tone at rest (Immordino-Yang & Yang, 2013) or to sensitivity to heartbeats and interoceptive sensations.

### *A Prospective Connection to Mental Health*

In addition to their theoretical implications, these findings provide evidence that the effects of cultural practices and the acquisition of cultural values on the experience of social emotion and self may be measurable in neurobiological experiments. Tying back to the theme of this volume, they can also by extension suggest that because emotions are a central part of mental health, a cultural neuroscience of social emotion could possibly inform questions about cultural effects in the social–emotional sequelae of mental illnesses, treatments, and psychiatry (Henningsen & Kirmayer, 2000).

For example, it is possible that the findings with regard to neural embodiment may relate to the cultural differences between Westerners and Easterners sometimes reported in the prevalence of somatoform disorders (Chentsova-Dutton et al., 2007; Parker, Cheah, & Roy, 2001; Ryder et al., 2008). In particular, Immordino-Yang and colleagues found that the magnitude of BOLD activation in the dorsal anterior insula, a visceral somatosensory region, was unrelated to the strength of emotional experience individuals reported in China, although it was strongly related in matched groups of American young adults (both of Asian descent and not; Immordino-Yang et al., 2014). Because somatoform disorders' key symptom is the dissociation between somatic manifestations of emotion and emotion awareness, these findings could possibly help explain the relative vulnerability of East Asians to these disorders, as well as Westerners' tendencies to assimilate embodied sensations into their psychological disorder. That is, perhaps the Chinese participants were experiencing the sensation of the embodied reaction and the strength of their emotional feeling as separate, whereas Americans may have been more likely to experience these as integrated or undifferentiated. These ideas are intriguing and present an alternate interpretation of the finding that Chinese individuals tend to talk more about their bodies when they are depressed (Parker, Cheah, & Roy, 2001; Ryder et al., 2008), although much more work is needed.

### *An Early Connection to Cultural Identity*

The ideas and findings presented here also suggest the possibility that an individual's natural sensitivity to visceral sensations may predispose him or her toward identifying with a culture whose norms for reliance on visceral sensation during the experience of social emotion are consistent with the individual's level of visceral sensitivity. Immordino-Yang and colleagues set out to test whether this might be the case for Chinese American bicultural adolescents living in a predominantly East Asian neighborhood in Los Angeles, and for Latino-American bi-cultural adolescents living in a predominantly Latino neighborhood. Using a heartbeat detection task, there was a cultural group interaction on the relationship between heart-beat detection accuracy and cultural identity. Specifically, Asian adolescents who could more accurately feel their own heartbeats reported on a separate acculturation questionnaire that they identified less strongly with Asian culture, and the reverse was also true: Adolescents who could not accurately feel their own heartbeats reported having a strongly "Asian" identity (Figure 8.2; Immordino-Yang & Yang, 2013b). By contrast, Latino adolescents showed the opposite pattern: those with better interoceptive accuracy reported being *more* strongly identified with Latino culture (Cheng, Yang, Hobeika, & Immordino-Yang, 2015). Whether the youths' ability to become consciously aware of their own heartbeats represented the cause or the effect of their self-identification with a cultural set of values is unclear, but given that there are limits to the developmental plasticity of visceral interoception in the brain, it is likely that youths' natural sensitivity to the sensation of their heartbeats steered them toward adopting a cultural identity that aligned with their embodied experience of social emotion. Future investigations will explore the robustness of this finding, its extension to other adolescent bicultural groups not of Asian and Latino descent, and its potential modulation by cultural priming.

## Benefits and Challenges of Incorporating Cultural Social Science Into Social-Affective Neuroscience and Vice Versa

The neuroscientific study of emotion can be used by cultural psychologists and biologically oriented anthropologists to understand more about the biological bases of emotion processing in order to refine models and theories of the role of emotions in social life and to ensure that psychological and anthropological theories and models are biologically plausible. The underlying premise of this argument is that because all social functioning is biologically based, understanding something about the logic of the

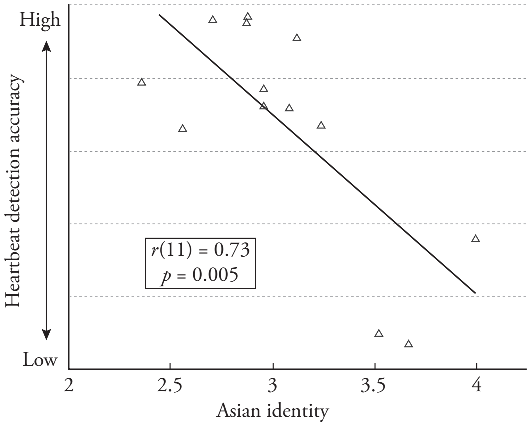

**Figure 8.2** In a study of Chinese American low-SES adolescents aged 14 or 15 years from Los Angeles, participants who claimed to identify more strongly with Asian culture on a questionnaire were less accurate at feeling their own heartbeats in a separate heartbeat detection task. This finding suggests that perhaps bicultural Asian American youth who are naturally more sensitive to visceral sensations may identify more with American culture because American culture values "gut feelings," whereas Asian culture values a more cognitive, other-oriented style of reacting in social situations. This early finding has now been corroborated with a larger sample and has been demonstrated in the opposite direction for Latino adolescents, for whom greater interoceptive accuracy is associated with *stronger* identification with Latino identity.

biological mechanisms underlying social–emotional development could therefore usefully constrain cultural models and research and vice versa: Cultural models and descriptions could help to ensure the real-world validity and generalizability of proposed neurobiological mechanisms. One complementary benefit of this approach will be that cultural psychologists can use their knowledge of development and group differences to help neuroscientists shape experimental questions and designs so that the findings will be maximally relevant to cultural questions. The more aligned neuroscientific research is with sociocultural research questions and models, and the more biologically plausible the sociocultural research questions and models, the more productive the contributions of each field will be.

At the same time, one important consideration in applying neuroscientific techniques to the study of emotion in cultural contexts is that neuroscience is inherently an experimental science, and whereas cultural psychology shares this characteristic, anthropological studies generally do not. The techniques for neuroscience research, especially neuroimaging, are constrained by experimental designs with control conditions and active conditions, and they subject participants to highly unnatural activities (e.g., lying still on one's back in the dark inside a loudly banging donut-shaped MRI scanner while one faithfully repeats a particular task tens to hundreds of times). Electroencephalography (EEG) research, which is more portable and less expensive, also requires that a participant reliably engage in multiple sequential trials of the same mental task (typically up to 100 trials) so that electrical signals from the brain can be averaged across these trials to identify the neural signal among the other sources of electrical noise (e.g., muscular activity in the scalp or face). Because no technology currently exists that allows researchers to study with precision the neurobiological correlates of culturally shaped behavior and thinking in natural contexts, the interpretations of cross-cultural neural findings can be complicated, especially because it is difficult to know how each cultural group interpreted and carried out the required task. Existing neuroimaging techniques do not currently provide a useful way to observe the emotional dimensions of ongoing, natural activity among individuals going about their daily business in a cultural setting. Nonetheless, a cultural neuroscience of emotion is possible. Some central interdisciplinary issues and recommendations are discussed next.

### *The Importance of Reconciling Theoretical Approaches and Models From Social Scientific Cultural Studies With Those From Neuroscience and Vice Versa*

One important way that a cultural perspective can be productively integrated into neuroscientific research agendas, or that a neuroscientific perspective can inform social-scientific cultural studies, is via the exchange of productive theoretical models. For new discoveries about cultural group differences in neural and psychological functioning to have their full impact and be fully understood, social scientists and neuroscientists need to debate the general principles that the findings reveal, and from there to derive testable hypotheses for both social scientific and neuroscientific studies. In bringing disciplines together to innovate in research, this updating of theoretical models is often neglected. Often, social scientists and neuroscientists alike, caught up in their zeal for new and exciting information and seeing the desperate need to innovate in their research, either overlook the importance of theory building or, conversely, discount potentially important new findings because they contradict established theories.

### *An Example of a Useful Theoretical Distinction: Emotions Versus Feelings*

One example of a theoretical contribution from neuroscientific measurements of emotion that is relevant to cultural studies is the distinction that neurobiological models make between emotion and feeling (Damasio, 2003). Whereas the term "emotion" refers to the changes in bodily and mental states that occur automatically as concerted packages in response to environmental or internal triggers (e.g., memories), "feelings" involve sensations and interpretations, conscious or nonconscious, of emotions that have already happened or are ongoing. Consider, for example, a student who is nervous about an upcoming math test. Whether this student is in China, Germany, South America, or the United States, she may gradually become aware of a knot sensation in her stomach, a headache, or an overall tenseness in her body. In this scenario, the bodily tenseness is automatically, nonconsciously induced by thoughts of the upcoming test, and it constitutes what has been called the "emotion" proper (Damasio, 2003). By contrast, the student's ability to subsequently become aware of this tenseness, to "feel" it as a culturally situated phenomenon and to attribute its cause to the perceived societal value of excelling on math tests, reflects more complex cognitive processing and even sometimes meta-awareness on her part (Barrett et al., 2004; Immordino-Yang, 2010; Immordino-Yang, Christodoulou, & Singh, 2012)—what has been described as the process of cognitively constructing an emotional feeling (Barrett, 2009; Damasio & Carvalho, 2013).

Notably, the distinction between emotions and feelings in the affective process has not generally been made in cultural research because cultural research on emotion processing is usually concerned with either nonconscious bodily changes (neurobiologically speaking, the "emotion") or the impact of these bodily changes on cognition, behavior, and meaning-making (neurobiological speaking, the "feelings"), but not often with both (for an exception, see Soto, Levenson, & Ebling, 2005). Neuroscientific research has been able to disentangle emotions, which happen first, from feelings, which happen later (e.g., Damasio et al., 2000). Psychophysiological methods have also been used to probe the role of arousal attributions to social emotional feelings (Mendes, Major, McCoy, & Blascovich, 2008), including classic studies of cultural effects in psychophysiological responses (Averill, Opton, & Lazarus, 1969; Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000; Levenson, Ekman, & Friesen, 1990). For an interdisciplinary research field of cultural social-affective neuroscience to move ahead, both measures of emotions and feelings need to be taken into account because culture may very well impact emotion and feelings via distinct (albeit mutually influential) mechanisms. Alternatively (or, in addition), it is possible that culture may influence the relation between emotions and feelings—that is, the way embodied reactions are subjectively perceived and conceptualized (Barrett, 2006; Immordino-Yang, 2010). The existence of this layer of dynamic complexity is hinted at in Immordino-Yang's early cross-cultural findings, described previously: There were no differences in the magnitude of BOLD activity or in the strength of social emotional feelings across the three cultural groups. Instead, the cultural differences were found in the relations between neural activity and participants' experienced feelings (Immordino-Yang, Yang, & Damasio, 2014).

Another important implication for cultural studies is that because emotions happen before feelings, feelings have the possibility of ongoing conscious and complex cognitive and affective elaboration and deliberation. That is, feelings are not necessarily automatic in the way that emotions are automatic. It is certainly possible to regulate emotion indirectly by reshaping one's cognitive appraisal of a situation or by effortfully suppressing the emotion response (Gross, 2008), and in fact there are already neural studies demonstrating cultural differences in these and related processes (e.g., Cheon et al., 2011). However, once an emotion has been induced, individuals' abilities to correctly recognize and adaptively attribute the causes of their emotions may be more flexible and acculturated than their abilities to regulate the emotional reaction itself. For instance, for the math student mentioned previously to understand that her embodied sensations relate to the upcoming math test and not to a developing viral infection, and then for her to frame these feelings in a productive and culturally appropriate way (e.g., as reflecting an exciting challenge rather than a personal threat; Cooley & Klinger, 1989), will be important for her academic success and social well-being. For instance, American students have been shown to regulate their test-taking anxiety more effectively by reflecting beforehand on the implications of the test for their life more broadly (Ramirez & Beilock, 2011), whereas Chinese students may more effectively manage their test-taking anxiety by cognitively suppressing the anxious feeling (Frenzel, Thrash, Pekrun, & Goetz, 2007; Pekrun, Goetz, Titz, & Perry, 2002). Studying such cultural variation in affective processing both at the level of the emotion itself and at the level of the ensuing feeling may help cultural neuroscience researchers to understand how cultural values and norms shape social affective processing—both the appraisal/emotional reaction sequence and the process of constructing an experience of these reactions (feelings).

### *Contributions to Understanding the Impact of Culture on Nonconscious Aspects of Emotion Processing*

Another benefit of incorporating insights from neurobiological findings into cross-cultural research designs and theories is that neurobiological mechanisms provide a window into differences in mental processing that occur below the level of conscious awareness (Immordino-Yang & Sylvan, 2010), even in the absence of measurable behavioral distinctions (Chiao, Cheon, Pornpattananangkul, Mrazek, & Blizinsky, 2013). The lack of methods for systematically investigating the aspects of cognition that are nonconscious has led to a strong bias in social science research toward an emphasis on the dimensions of emotions (as they relate to cognition, social processing, decision-making, and identity) that are most readily measurable by external observation, behavioral outcome, or conscious report. Although these measures are essential for understanding many aspects of human behavior, they may be unable to provide a thorough explanation of the underlying processes that give rise to emotionally relevant, socially motivated behavior. To date, there has been a paucity of tools to probe the contributions of these underlying processes. Neuroimaging research on emotion has the potential to help address this gap by providing new insights into the workings of nonconscious biological mechanisms (Immordino-Yang & Sylvan, 2010).

For example, work on the brain's activity during rest and social emotion suggests that people may unconsciously shift their attention inwardly, away from the immediate physical context, in order to build more abstract construals of an emotional situation (Pavarini, Yang, Schnall, & Immordino-Yang, 2015; Trope & Liberman, 2010). These shifts in attention may facilitate the induction of future-oriented mindsets, including a sense of intrinsic motivation and emotions such as inspiration, or a profound sense of purposeful achievement focus, both of which neuroimaging research suggests involve neural processing that happens below the level of conscious awareness (Immordino-Yang & Sylvan, 2010; Murayama, Matsumoto, Izuma, & Matsumoto, 2010). Interestingly, the early analyses reveal robust cultural differences in the emotion-related activation of these neural systems (e.g., the medulla), despite the fact that these systems cannot be consciously controlled and despite that these systems are also responsible for regulating basic homeostatic mechanisms.

### *Contributions to the Creation of Natural Behavioral Indices of Emotion Processing*

One area of neurobiological research that holds promise for translation into natural cultural settings, but is still quite exploratory, comes from neurobiological studies of relations between brain activity during fMRI scanning and natural variation in participants' spontaneous natural behaviors observed in another context, such as a private interview (Immordino-Yang, 2013). These studies suggest that certain behaviors can be indirect indicators of particular psychological and neural states, suggesting potentially that social science researchers could be taught to identify these behaviors and would therefore not need neuroimaging to infer some types of information about their subjects' neural processing.

For example, in an ongoing series of experiments, participants describe their genuine feelings about social stories in a private videotaped interview and then react again to the same stories in the fMRI scanner (Immordino-Yang, et al., 2009; Saxbe et al., 2013; Yang et al., 2013). Early results of a study of participants' nonverbal interview behavior reveal that participants tend to avert their gaze away from distractions in the immediate environment when they report feeling inspired or reflective in the interview (Yang, Pavarini, Schnall, & Immordino-Yang, 2012). For example, they tend to turn their eyes to the blank ceiling or nondescript wall, to refrain from shifting posture or gesturing, and to incorporate long pauses into their speech. Interestingly, individual differences in the extent to which participants reported becoming inspired by social stories correlated with their tendency to avert their gaze when deliberating on the story's meaning. In addition, eye gaze aversion also correlated with individual differences in neural activity in the subsequent fMRI task, suggesting that eye gaze may be a behavioral indicator of certain patterns of thinking and certain neural systems activating (Pavarini et al., 2015). Although this research is in its early stages, it does provide a tantalizing suggestion that neuroscientific evidence could potentially be used to identify natural behavioral indicators known to be associated with particular neural states—in this case, instances of effortful internal reflection in natural cultural contexts (Immordino-Yang et al., 2012). Future work may flesh out this insight in order to determine whether it provides a useful tool to support social scientific researchers in developing more effective behavioral indexes of internally focused, reflective mental processing.

## Into the Future: Integrating Cultural and Neuroscientific Perspectives to Study Social Emotion

Given the recent surge of advances in social and affective neuroscience, coupled with an increased need globally for understanding cultural effects on social and emotional functioning, it is time to begin a serious conversation about how social scientists and social affective neuroscientists can enter into productive research collaborations. In the future that I envision, traditional anthropological methods are in no way obsolete; neither am I advocating that sociocultural explanations be replaced by biological ones. It is unreasonable and unnecessary to expect ethnographers, for example, to become amateur neuroscientists. However, anthropological theories and neuropsychological theories must be compatible, and cross-disciplinary grappling with inconsistencies or contradictions could improve thinking in both domains. Using neuroscientific conceptions in conjunction with culturally sensitive approaches might make it possible to systematically probe the conscious and nonconscious biopsychological mechanisms by which human beings experience and make meaning of their social and emotional lives. In turn, formulating and testing hypotheses grounded in neuroscience using culturally situated methods would also inform advances in neuroscientific thinking by helping neuroscientists to learn about the ways that brain findings play out in real-life settings and across diverse groups of people.

In order to move forward, one of the major challenges facing researchers now is to reconcile the new neuroscientific findings on social, affective, and self-relevant processing with established cultural psychological and anthropological evidence and with new evidence concerning how genetic differences lead to phenotypic propensities (a topic that is the basis of Chapter 21 in this volume). Designing research and theories that begin to span these levels of analysis is an intellectually formidable task but one that is centrally important for the future of cognitive, social, and affective neuroscience. Humans are, by our very biology, a cultural species; to understand how the human brain creates the human mind, then, absolutely requires integrating a cultural perspective. By bridging between cultural processes at the level of the mind and naturally occurring neurobiological variability across humans, we can improve the validity and generalizability of neuroscientific research and inform understanding of the biological constraints undergirding anthropological and psychological studies of the mind. Cultural neuroscience—an interdisciplinary field poised between social-affective and cognitive neuroscience, psychology, and anthropology—is well situated to begin reconciling these levels of evidence.

In conclusion, social emotions are both neurobiological and psychological phenomena. To understand these emotions, therefore, we should strive to integrate a cultural perspective into social emotion studies, both neurobiological and psychological. Among the first steps will be for interested cultural psychologists, psychiatrists, and anthropologists to become familiar with the range of approaches currently available in neuroscience, along with their promises and limitations, and to learn about neurobiological models of social and affective processing. In the other direction, social affective neuroscientists will need to become familiar with cultural models of sociality and with known cultural variation in values and norms for emotion processing. In this way, researchers from neuroscientific and from social scientific backgrounds could work together to develop novel methods to align traditional ethnographic and cultural psychological methods and measurements with neurobiological correlates and mechanisms of emotion. Such an approach would allow researchers from both backgrounds to more deeply probe the conditions under which particular emotions are induced in different cultural contexts and groups; potential differences in how these emotions play out and are felt; and how the development of healthy, culturally appropriate social emotions is shaped by experience, context, and biological predispositions. This is a difficult challenge because translating across and integrating disciplinary approaches is never straightforward. However, in my opinion, it will be necessary for the field to truly advance in understanding the inherently biological and cultural human mind.

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CHAPTER

9

# Cultural Neuroscience in South Africa: Promises and Pitfalls

Dan J. Stein, Joan Y. Chiao *and* Jack van Honk

**Abstract**

South Africa may be a particularly useful exemplar with which to consider some of the potential promises and pitfalls of cultural neuroscience. This chapter draws on our experience as scientists who have worked in the South African context, who have used both neuroscientific and social science methodologies, and who have wondered how best to integrate these often quite different perspectives. We begin by proposing a heuristic conceptual framework that articulates “classical,” “critical,” and “integrative” approaches to cultural neuroscience, and we then use this to exemplify promises and pitfalls of cultural neuroscience in South Africa and to map out a research agenda for the future.

**Key Words:** cultural neuroscience, South Africa, heuristic conceptual framework, methodologies, integrative

Cultural neuroscience seeks to investigate how bidirectional relationships between neurobiology and culture account for variations in cognition, affect, and behavior (Chiao, Cheon, Pornpattanangkul, Mrazek, & Blizinsky, 2013). It is motivated by two questions about human nature and its variations: How do cultural traits shape neurobiology, and how do neurobiological mechanisms facilitate the emergence and transmission of cultural traits (Chiao, 2009; Domínguez, Lewis, Turner, & Egan, 2009)? Although the possibility of such work has long been discussed, modern brain imaging, neurogenetics, and other neuroscience methodologies have recently provided key opportunities for such research (Chiao et al., 2010). Such methodologies can be used to explore a range of populations that go beyond the white, educated, industrialized, rich, and democratic (WEIRD) populations that are so often studied by biological psychology (Henrich, Heine, & Norenzayan, 2010).

South Africa may be a particularly interesting country in which to undertake cultural neuroscience (Table 9.1). Africa is of course the genetic home of all mankind, and some of the earliest cultural artefacts of our species have been found on the South African coast (Henshilwood et al., 2011). Modern populations range from the aboriginal San and Khoi populations to black and white populations that may each be fairly homogenous from both a genetic and cultural viewpoint and on to populations that are diverse from both a genetic and cultural perspective (Pickrell et al., 2012; Tishkoff et al., 2009). Although the dawn of democracy has meant that apartheid racial classifications are now seen as based on political ideology, they continue to serve as markers of enduring disparities (e.g., in health access) across groups (Stein, Williams, & Kessler, 2009; Williams et al., 2008).

In this chapter, we explore some of the promises and pitfalls of a research agenda on cultural neuroscience research in South Africa. We hope that this discussion serves not only to help clarify the directions and focus of a research agenda for those interested in taking it forward but also to provide a conceptual framework that is useful for exploring analogous issues in other contexts. The chapter

**Table 9.1 Cultural Neuroscience in South Africa**

| Level of Analysis | Key Factors of Interest |
|---|---|
| Ecology | Historical conflict<br>Economic conditions<br>Infectious disease<br>Population density<br>Dietary habits |
| Culture | Individualism–collectivism<br>Social network<br>Urban–rural<br>Group identification<br>Power distance<br>Time orientation |
| Gene (specific polymorphisms, genome-wide association studies) | *5-HTTLPR*<br>*DRD4*<br>*COMT*<br>*OPRM1* |
| Neurocircuitry | Prefrontal–amygdala circuitry<br>Cortical-striatal-thalamic-circuitry (Default mode network)<br>Reward circuitry |
| Cognitive-affective Processes | Decision-making<br>Emotion Perception<br>Emotion Regulation<br>Reward Processing |

draws on our experience as scientists who have worked in the South African context, who have used both neuroscientific and social science methodologies, and who have wondered how best to integrate these often quite different perspectives. We begin by proposing a heuristic conceptual framework that articulates "classical," "critical," and "integrative" approaches to cultural neuroscience, and we then use this to exemplify promises and pitfalls of cultural neuroscience in South Africa and to map out a research agenda for the future.

## A Conceptual Framework

Stein (1991, 2008) put forward a heuristic schema that contrasts different conceptual approaches to science and language, as well as to medicine and psychiatry. Although the framework draws on key positions that have been established in philosophy, it may not successfully capture the arguments of any particular author. Instead, it is intended to provide a useful map for comparing and contrasting a number of important conceptual positions and so perhaps provide theorists and scientists some directions for avoiding key errors when thinking through or planning a research program.

A "classical" approach can be traced from early philosophers such as Plato to the more recent Anglo-American school of logical positivism. This view emphasizes that science observes and draws relationships between the phenomena of the world, that language involves an objective process of verification in order to determine the veracity of particular statements, and that psychological phenomena should be approached in much the same way as are physical phenomena—relying on an approach that emphasizes operational definitions and that uncovers the universal laws which explain relationships between observed phenomena.

A "critical" approach can be traced through the work of many philosophers, often working in continental Europe, who have taken a contrary position to the classical one. This view emphasizes that science is a human practice that is theory-bound and value-bound, that language involves a subjective process of validation in order to determine the meaningfulness of particular statements, and that psychological phenomena are entirely different from physical phenomena—they rely on the understanding (*verstehen*) of context rather than on explanation (*erklaren*). This view also emphasizes that the psychological cannot simply be reduced to the physical.

An "integrative" approach is also found in the work of a range of philosophers (Bhaskar, 1978, 1979). This approach argues that science is a social activity but that it also discovers real mechanisms; that language embodies the metaphors used in a particular time and place but that it can also provide precise accounts of the structures and mechanisms of the world; that the investigation of psychological phenomena requires both verstehen and erklaren; and that the human sciences provide explanations which address a range of different levels of reality, ranging from the molecular to the psychological and sociological (Kendler, 2011).

Here is not the place to provide a detailed defense of the integrative position. Nevertheless, one particularly relevant point for scientists is that the integrative position arguably provides a powerful explanatory model of the actual activities of scientists. In particular, although science is clearly a social process and relies on the constructs of a particular time and place, it is also an attempt to uncover real explanatory mechanisms. Furthermore, psychological science, although different in important ways from physical science, has many overlaps with other disciplines, and although it uncovers psychobiological mechanisms, it rarely attempts to reduce entirely the psychological to the physical.

## Pitfalls

The use of solely a classical or critical perspective for conceptualizing cultural neuroscience entails a number of pitfalls, which can be exemplified in the South African context. A classical approach that fails to recognize different levels of explanation, ranging from the molecular to the sociological and anthropological, may hypothesize that racial categorizes can be entirely explained in terms of particular brain neurocircuitry or molecular entities, or otherwise essentialize the complexity of culture (Choudhury, Nagel, & Slaby, 2009; Denkhaus & Bös, 2012; Martínez Mateo, Cabanis, Cruz de Echeverría Loebell, & Krach, 2012; Martínez Mateo, Cabanis, Stenmanns, & Krach, 2013; Slaby, 2010). In the South African setting, such reductionism risks unfounded reification of the social constructions put in place by apartheid ideology. Any particular variable that is examined across population groups in South Africa may well reflect social disparities rather than any neurobiological essences that correlate with populations per se.

Conversely, a critical approach that claims that all psychological phenomena merely reflect the social constructions of a particular time and place runs the risk of ignoring the possible existence of universal psychobiological mechanisms, including those responsible for diversity. In the South African setting, such relativism risks failing to recognize the importance of evolved psychobiological mechanisms that contribute to understanding variation in cognition, affect, and behaviors and the effects of such variation on health and illness. There are likely to be important overlaps in cognitive–affective processes across different South African groups, which appear despite the historical and ongoing differences in contexts that individuals experience. Furthermore, although it is important not to essentialize population groups, these may be a key marker of health disparities in the South African setting (Ncayiyana, 2007).

Indeed, avoiding the perils of both reductionism and relativism in approaching population groups in cultural neuroscience research remains important, both in the South African context and more broadly. It is useful to recognize the crucial and tragic errors that theorists and scientists have made in their work on racial constructs in a range of different contexts. A eugenics movement, which labels some genes as "good" and other as "flawed," was drawn on by the architects of apartheid. Early European colonial science invariably viewed Africans as "lesser" (Dubow, 1995; Gould, 1981). In psychology and psychiatry, such authors have taken a range of erroneous positions, arguing, for example, that Africans did not experience depression because they did not have the sophisticated mental structures and operations that were necessary for feelings such as guilt (German, 1972; van Ommen & Painter, 2008).

The use of racial constructs in South African and other health research remains an ongoing matter of controversy (Bloche, 2004; Caulfield, Fullerton, & Ali, 2009; Foster, 2009; Wilkinson & King, 1987). Although the use of such constructs may serve a practical tool, such utility may be taken for granted rather than rigorously assessed; a "rational medicine" requires a rational approach to addressing the nature of population group disparities and inequality in health and society more broadly (Braun et al., 2007; Fullwiley, 2007). On the one hand, it can be argued that population group remains a poor proxy for social and health disadvantage, whereas on the other hand, the case can be made that more powerful methods than the use of racial constructs exist for addressing population structure (Shields et al., 2005; Wang & Sue, 2005). Some have argued that there should be a presumption against the use of racial constructs, unless they are able to contribute meaningfully to improving health (Bloche, 2004). Certainly, there is a need for a sophisticated critique of such constructs, which allows an integration of both biological and cultural data (Gravlee, 2009).

Another example that may help illustrate the pitfalls of reductionism and relativism is controversy about the notion of posttraumatic stress disorder (PTSD), both globally and in the South African context (Stein, Seedat, Iversen, & Wessely, 2007). A classical approach to psychiatric disorders may view these as natural kinds that can be operationally defined using necessary and sufficient diagnostic criteria, much as a square can defined in this way. In this view, PTSD is considered a set of symptoms that are associated with objectively defined traumatic events and invariant from time to time and place to place. In contrast, a critical approach to psychiatric disorders may view these as social constructs that vary over history and geography, much like what is considered to vary from culture to culture. In this view, PTSD is merely a social construction, which may be employed for particular sociopolitical reasons (Young, 1995).

A potential weakness of the classical approach to PTSD is that trauma responses are viewed as natural kinds that are somehow fixed by biology, thus ignoring the variable ways in which society and culture can influence the subjective experiences of trauma and the expression of subsequent symptoms (Stein et al., 2007). Such a biomedical model may also deflect attention away from important sociopolitical efforts to prevent violence and away from a range of potentially useful, nonmedical interventions to relieve distress after trauma. On the other hand, a potential weakness of the critical approach to PTSD is that it runs the risk of downplaying important similarities in symptoms and psychobiology in all people with PTSD and, by ignoring the medical model, failing to offer effective treatment. A model that focuses entirely on social determinants may deflect attention away from a comprehensive understanding of how psychobiological mechanisms account for both similarities and differences across individuals and societies in response to trauma.

An integrative approach to PTSD emphasizes the importance of both mechanisms and meanings in the development of this condition. In this view, a comprehensive approach to trauma should be based on not only an appreciation of the underlying associated psychobiological mechanisms that lead to PTSD symptoms but also an understanding of the specific psychosocial context within which the response to trauma is embedded and that affects the experience of trauma and the expression of subsequent responses. Thus, although some have argued that apartheid society was essentially “sick” and “traumatic,” necessarily resulting in psychopathology, a more nuanced view also emphasizes the resilience of people who partook in the struggle against apartheid. A view that focuses on the evolved psychobiological mechanisms (e.g., disruptions in fear processing) underlying both similarities and differences in experience and outcomes in those who lived through apartheid is needed to explain a broad range of complex phenomena, such as why some individuals are more vulnerable and others more resilience to developing PTSD after trauma, why trauma survivors with an ideological commitment to their cause seem less likely to complain of stress-related psychiatric symptoms than those without such commitment, and why PTSD is seen not only in survivors of gross human rights violations but also in perpetrators (Kaminer, Stein, Mbanga, & Zungu-Dirwayi, 2001).

## Promises

Indeed, an integrative approach that brings together aspects of the classical and critical approaches may be particularly useful in providing a conceptual framework for the underpinning of cultural neuroscience. Although this approach would certainly acknowledge cultural diversity in cognitions, affects, and behaviors, it would also emphasize the possibility of uncovering real psychobiological mechanisms that account for both similarities and differences between individuals; cultural neuroscience is equally concerned with both phenomena (Chiao & Blizinsky, 2013). Several such mechanisms, and their interactions, appear relevant for cultural neuroscience as it advances in South Africa.

First, there may indeed be broad differences (as well as overlaps) in cognitive–affective processes across groups. In the South African setting, for example, collectivism may possibly be more characteristic of traditional communities, whereas individualism may possibly be more characteristic of urbanized groups. Racial identification, or the extent to which people identify with their racial or ethnic group, may serve as an important factor in shaping psychological processes of population groups within South Africa (Phinney, 1992). Cultural values associated with power distance, or the extent to which social hierarchical or egalitarian social interactions are maintained and transmitted across generations, may be another factor affecting South African populations (Hofstede, 2001; Sidanius, Levin, Federico, & Pratto, 2001). Cultural factors that are related to time orientation, specifically long-term or short-term orientation, may also play an important role in influencing health across different South African population groups (Hofstede, 2001; Zimbardo & Boyd, 2008).

Second, such broad differences (and overlaps) in cognitive–affective processes across population groups due to diversity in cultural values may be underpinned by differences (and overlaps) in neural circuitry. Neuroimaging evidence indicates that cultural collectivism is associated with increased medial prefrontal cortex (mPFC) response to contextual self-representations, whereas cultural individualism is associated with increased mPFC to trait-like self-representations (Chiao et al., 2009). At the same time, individuals with broader social networks are characterized by larger amygdala (Bickart, Wright, Dautoff, Dickerson, & Feldman Barrett, 2010), and individuals living in large cities have more activated amygdala in response to fearful stimuli (Lederbogen, Kirsch, Haddad, & Streit, 2011). Among African Americans and Caucasian Americans in the United States, racial identification has been shown to modulate neural responses during empathic processing within cortical midline structures, including the mPFC, the posterior cingulate cortex (PCC), and the anterior cingulate cortex (ACC), as well as the medial temporal lobe (Mathur, Harada, & Chiao, 2012). African Americans who typically show high racial identification show increased neural response within mPFC, PCC, and ACC, whereas Caucasian Americans who typically show low racial identification show increased response with parahippocampal cortex during empathic processing. Expectations for social hierarchy or egalitarian social norms may also alter neural processing. For instance, when living in a hierarchical culture, people show increased recruitment of theory of mind mechanisms, such as left temporoparietal junction, when empathizing with the suffering of group members compared to people living in egalitarian cultures (Cheon et al., 2011). Given similarities in the sociopolitical history of intergroup conflict and reconciliation within the United States and South Africa, it is possible that common cultural factors explain, in part, neural variability when thinking or feeling about same- and other-race people. In the South African context, however, there has to date been very little work on addressing differences in neuronal structure and function that underlie distinctions in cognitive–affective processes across population groups.

Third, such differences (and overlaps) in neuronal structure and function may in turn be underpinned, at least in part, by differences (and overlaps) in a range of genetic and environmental mechanisms. Thus, for example, it has been found that functional polymorphisms in the serotonin transporter may contribute to the extent of amygdala activation in response to fearful stimuli (Hariri et al., 2002; Murphy et al., 2013). A range of other molecular variants may contribute to variance in neuronal circuitry. Furthermore, environmental stressors and supports may interact with such genetic and molecular factors in order to influence brain structure and function (Canli et al., 2006). To date, there has been very little work in any low- and middle-income countries, including South Africa, examining genetic and environmental contributors to diversity in neuronal structure (Hoare et al., 2012).

Fourth, it may be relevant to consider not only proximal but also distal factors that contribute to diversity in cognitive–affective structures, neuronal circuitry, and molecular mechanisms in the production of adaptive behavior (Chiao & Blizinsky, 2010; Nesse & Stein, 2012). A comprehensive understanding of the diversity of cognitive–affective processes that produce normal and pathological psychological phenomena (e.g., anxiety and depression) would seem to require a clear understanding of their evolution and adaptive value (e.g., an understanding of how fear alarms are adaptive) across cultural contexts. For instance, Chiao and Blizinsky suggested culture–gene coevolution of individualism–collectivism and the serotonin transporter gene (*5-HTTLPR*). Groups that show increased cultural collectivism also show increased prevalence of the short allele (S) of the serotonin transporter gene but reduced prevalence of anxiety and mood disorders. In South Africa, there may be a greater frequency of long allele (L) carriers within the population, but the evolutionary, neurobiological, and cultural significance of this finding remains unknown. In the South African context, although statements about the adaptive nature of particular genotypes run the risk of being highly contentious and even inflammatory, there is some rigorous work along these lines (Bains, 2013). Given the unique genetic and cultural diversity of the South African population, it is possible that unique gene–environment pathways may characterize and predict mental health in South Africa.

Fifth, it is important to understand the complex ways in which different kinds of levels interact (Ghaemi, 2003; Kendler, 2011). Thus, in work on anxiety disorders, there are data on how cognitive–affective processes are influenced by both genetic and environmental factors, on how genetic factors contribute to distinctions in brain imaging findings, and on how both pharmacotherapy and psychotherapy are able to normalize neuronal circuitry (Stein, 2006). However, few, if any, studies have rigorously examined the effects of different psychopharmacological agents on brain and behavior across cultures. There is also a need to understand how the brains and minds of people from different cultures respond to different kinds of psychotherapy intervention and social communication approaches. Although ideally scientists hope to move from the bench to the bedside and then to the community as a whole, it is not unlikely that a more complex approach is needed, with both bedside and community influencing bench experimental design.

## A Research Framework

Going forward, then, it is crucial for a research framework for cultural neuroscience in South Africa to investigate cognitive–affective processes that differ (to some extent) across population groups and at the same time are tractable to analysis in terms of neuronal circuitry and molecular mechanisms and that therefore advance our understanding of both endophenotypes (genetically inherited constructs that help explain phenotypes) and exophenotypes (socially created phenomena that help explain phenotypes) (Stein, Lund, & Nesse, 2013).

Consider, for example, the kinds of sounds made by individuals from different population groups when using different languages. Differences in verbal structure and content are of course of great interest to linguists. However, from the perspective of cognitive neuroscience, diversity in word content across groups may not be as informative as exploring other cognitive–affective processes. For example, differences in the kinds of metaphors and idioms employed by different groups in South Africa may reflect key differences in local endophenotypes and/or exophenotypes. Thus, there are rich opportunities for cultural neuroscience research in South Africa.

Although all psychological phenomena are arguably underpinned by both nature and nurture, a focus on endophenotypes necessarily pays more attention to genetic contributors to understanding diversity in cognitions and affects, and a focus on exophenotypes necessarily pays more attention to social contributors to understanding diversity. Given the wonderful genetic diversity in South Africa, there is an argument for focusing research on endophenotypes. At the same, given South Africa's divergent cultures and the remarkable history of apartheid and the struggle against it, there is also a strong argument for focusing research on exophenotypes. A comprehensive research program should likely include both perspectives, and the interaction between them, so that questions of both brain–mind in culture and culture in brain–mind (Domínguez et al., 2009) as well their complex intersection can be addressed.

Consider, for example, the Truth and Reconciliation Commission (TRC) of South Africa. After democracy came to South Africa, there was an important need to address the human rights abuses of the past. The TRC took an approach of reparative rather than retributive justice. Although many perpetrators were white and asking for amnesty, and many victims were black and being asked for forgiveness, the complexities of the South African situation meant that there was no simple relationship between population group and such processes. However, key cognitive–affective processes during the TRC were empathizing with those who testified and forgiveness of perpetrators by victims (Stein et al., 2008).

Indeed, the TRC provided the opportunity for an approach to PTSD that both emphasized the idea that survivors deserved compensation for their trauma (a medical model) and also emphasized that acknowledgment of the trauma was more important than retributive justice (a model that emphasized resilience). Clearly, it is important not to ignore the real needs of those suffering from PTSD. On the other hand, by focusing on resilience, the TRC arguably offered acknowledgment to many individuals and provided a useful social model of how to address mass trauma (Stein, Kaminer, Zungu-Dirwayi, & Seedat, 2006).

Levels of empathy and forgiveness differ markedly across individuals in the South African context (Allan, Allan, Kaminer, & Stein, 2006). Thus, there is a real opportunity locally to study the psychobiology of these processes across individuals (i.e., the relevant endophenotypes) (Stein & Kaminer, 2006). On the other hand, in the South African situation, diversity in phenomena such as empathy and forgiveness may also be based on differential exposures to a range of psychosocial variables, including exposure to different religious and spiritual ideas (e.g., about Ubuntu) and commitment to social justice; thus, there is an important opportunity to study the relevant exophenotypes. Ultimately, it is important to integrate these different sets of research and, as discussed previously, to provide multilevel explanations.

The origins of *Homo sapiens* in Africa remind us of a range of universal commonalities in cognitive–affective processes across the different populations of the world. It seems clear, for example, that basic emotion expression and perception are largely shared throughout the world. At the same time, the wide range of diversity (e.g., in cognitions, affects, behaviors, and health outcomes) in Africa reminds us of the sophisticated shaping of psychobiological mechanisms in various ways from time to time and place to place. Genetic diversity in Africa is of course the highest in the world. In addition, the cultures in Africa are full of rich variation.

Thus, South Africa and Africa are potentially important sites of future cultural neuroscience research. Such research could usefully focus on both healthy populations and individuals with neuropsychiatric illness. There is scope within South African cultural neuroscience for studying both neurogenetic disorders (Terburg et al., 2012) and culture-bound phenomena (Niehaus et al., 2004). Similarly, it may be productive to study not only local psychotropic agents (Terburg et al., 2013) but also culturally relevant adaptations of individual psychotherapeutic and social interventions (Remien et al., 2013). There is a long history of remarkable contributions from South Africa in psychiatry and clinical psychology, and with the emergence of the new tools that provide the foundations of cultural neuroscience, it is hoped that there will also be contributions in this area (Stein, 2012).

## Conclusion

This chapter described some promises and pitfalls for the development of cultural neuroscience in South Africa. A conceptual framework that distinguishes between different conceptual approaches to science, language, and medicine/psychiatry may be useful in highlighting the pitfalls of reductionism and relativism and also the potential of integrative multidisciplinary approaches. After all, debates about the promises and pitfalls of the emerging field of cultural neuroscience (Chiao et al., 2013; Choudhury et al., 2009) reflect older and broader debates in the philosophy of science and biology. A broad research agenda that deals with both proximal and distal mechanisms and that addresses endophenotypes and exophenotypes and their interactions, along with the relevant underlying neural circuitry and molecular mechanisms in healthy and ill populations, seems most attractive.

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# PART 3

# Cultural Neuroscience of Cognition

CHAPTER

# 10

# Cross-Cultural Differences in Memory

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## Abstract

This chapter reviews the literature on the effects of culture on memory, focusing on the comparison of Easterners and Westerners. The chapter opens with a consideration of the mechanisms through which culture can impact memory and then reviews the cognitive biases and strategies that can shape memory, including memory for objects versus background, memory for perceptual details, source memory, the use of categories in memory, and false memory. Next, the chapter presents evidence for cross-cultural differences in self-relevant, autobiographical, and emotional memory, and it discusses the neuroimaging literature broadly related to differences in self-construals across cultures. Throughout, the chapter adopts a developmental perspective with a focus on older adulthood, and it closes with a consideration of the health relevance of the study of memory across cultures with age.

**Key Words:** memory, long-term memory, cognition, culture, cross-cultural, aging, self

Although the influence of culture on socially relevant behavior has long been appreciated, it initially may strike one as surprising that culture can also permeate lower-level cognitive processes such as memory. Some aspects of memory are highly constrained and resource-dependent, such as working memory—the ability to keep information online and perform manipulations on it (e.g., mental calculations or rehearsing a list of items on a grocery list). However, other aspects of memory are highly malleable and can reflect the motivations and information processing strategies and biases of the rememberer. This aspect of memory is particularly rich in its ability to offer a window into the ways in which one envisions oneself as well as the surrounding environment.

The constructive nature of long-term memory became a focus of the field in the 1990s as controversy surrounding recovered repressed memories and eyewitness memory came to a head. This debate drew attention to the malleability of memory, with an appreciation for the ways in which present-day suggestions and motivations could impact the ways that one remembers the past (Loftus, 2005; Schacter, 1999). This perspective parallels neuroscience findings on the plasticity of memory such that memories appear to be reconsolidated upon retrieval, which puts them in a labile state subject to alteration (Tronson & Taylor, 2007). The focus on the constructive nature of memory also connects to the broader literature on plasticity such that experiences such as becoming a London taxi driver (Maguire et al., 2000) or learning to juggle (Draganski et al., 2004) sculpt neural circuitry. Culture can be conceptualized as a set of experiences that similarly mold the brain as a result of the repeated use and reinforcement of cultural perspectives and information processing strategies across the lifespan (Park & Gutchess, 2002, 2006). Although such ideas are intuitive to those steeped in an anthropological or culture-centered approach, there has been little research on the ways in which culture impacts cognition, suggesting that the potential for cultural influences in this domain has been underappreciated by the field of cognitive psychology or perhaps even the field of psychology as a whole (for a discussion of this point, see Bloch, 1998).

Culture has been suggested to shape cognitive processes through the operation of three mechanisms, working separately or sometimes in tandem. The framework by Gutchess, Schwartz, and Boduroglu (2011) suggests that cross-cultural differences in cognition may occur for three reasons. First, different cognitive *processes* are engaged. This means that different strategies are adopted by people across cultures (e.g., using taxonomic categories to organize information in memory) or that people process distinct elements of complex information (e.g., focal person vs. social context). Second, *content* differs, such that distinct information is stored and accessed by individuals from different cultures (e.g., object vs. background information). Third, the degree of *difficulty* differs, such that one task is more challenging and requires more resources for members of one culture compared to another. The first mechanism, differences in cognitive processes, has been the focus of most research thus far on cross-cultural differences in cognition and memory.

This chapter reviews the literature on how culture impacts memory, focusing on the different aspects and dimensions of memory. It begins by considering the cognitive biases and strategies that can shape memory, including attention to object and background, cross-cultural differences in source memory, the use of categories in memory, and false memory. It then reviews evidence for cross-cultural differences in the highly personal, subjective, and emotional aspects of memory that are relevant to one's past and motivational goals.

## Mechanisms for the Impact of Culture on Memory

Cultural perspectives impact the prioritization of particular cognitive processes. For example, the individualistic perspective of Westerners could contribute to their increased attention to objects and parts of the field, and their bias toward categorization, whereas the collectivist perspective of Easterners could play into their increased attention to field and context and focus on functional relationships (Nisbett & Masuda, 2003; Nisbett, Peng, Choi, & Norenzayan, 2001). These cognitive biases can shape memory. People are necessarily limited information processors, unable to simultaneously attend to and remember all aspects of complex environments. Thus, people select particular aspects of the world around them to process further. By creating an enduring trace of what has been selected for further processing, what is remembered reveals the values and priorities of a culture. As proposed by Gutchess and Indeck (2009), extensive experience in a culture can interact with memory processes in a number of ways. Not only can it direct attention in the environment, influencing, for example, how much one attends to a central focal object versus attending more broadly to the surrounding context, but also the lens of culture can affect the type of knowledge acquired (e.g., whether information is organized into taxonomic groupings and categories). This knowledge can then iteratively shape how new information is assimilated into the existing knowledge structure. Likewise, one's culture can convey strategies for processing information, such as organizing information by salient taxonomic categories, analyzing the singular features of an item, or considering its relationship to other elements. Cultural perspective can determine the types of details that are encoded into memory, such as the relevance of information to oneself. Also, as discussed later in this chapter, culture shapes not only these aspects of accurate memory but also the types of memory distortions that can occur.

It is also important to consider a developmental perspective in the study of memory across cultures. This is not just because of the particular health relevance of memory with age, as memory complaints and concerns rate high for even healthy older adults (O'Connor, Pollitt, Roth, Brook, & Reiss, 1990). The more vulnerable memory that occurs with advanced age also presents an opportunity in that older adults may illustrate the biases and influence of their culture more than younger adults due to limited cognitive resources or as an effect of the greater amount of time that they have spent immersed in a culture, practicing and being shaped by the information processing approaches emphasized by their own culture (Park & Gutchess, 2002, 2006).

## Memory for Object Versus Background

One of the initial cross-cultural studies of memory focused on differences in memory for objects and contexts (Masuda & Nisbett, 2001). After watching brief animated vignettes, Americans and Japanese described what they had seen. Americans' descriptions largely focused on the central object (e.g., the large fish swimming across the front of the scene), but Japanese descriptions included additional description of background elements, such as the color of the water or the position of the seaweed relative to the focal fish. The second experiment more directly assessed cultural differences in memory for background information. Recognition performance of Japanese was more impaired when backgrounds had been removed or changed, whereas Americans' memory for the focal object was relatively insensitive to the changes in the background.

Whereas the study by Masuda and Nisbett (2001) primarily relied on comparing cultures on hit rates—that is, correct recognition of previously presented old items—other research has emphasized the importance of incorporating measures of false alarms, incorrect responses to new items, in an analysis of receiver operating characteristics (ROC) curves. This approach allows for full investigation of the ability to discriminate old from new in memory, apart from the contribution of response bias—the tendency to disproportionately respond "old" or "new." Cultural difference in the recognition of objects did not emerge in an analysis of ROC curves; although testing items on a new background rather than the original old background decreased memory sensitivity for both Americans and Chinese, it did so to a similar degree for each culture (Evans, Rotello, Li, & Rayner, 2009). Thus, it is important to consider both memory sensitivity and response bias across cultures.

Cultural differences in attention to objects versus backgrounds may also inform the study of memory. Eye-tracking data reveal that Americans fixate to the focal object in a scene sooner and longer than do East Asians, whereas no cultural differences occur in fixations to backgrounds (Chua, Boland, & Nisbett, 2005; but for a failure to replicate, see Evans et al., 2009). Neuroimaging data also indicate that Americans process objects more than East Asians, with greater activation of lateral temporal regions associated with object processing (Gutchess, Welsh, Boduroglu, & Park, 2006). In contrast, circumscribed differences occur across cultures in regions associated with background processing. The findings with these methods emphasize the greater processing of objects by Americans, contrasting the earlier focus in the behavioral literature on East Asians' greater processing of background or context.

## Age Differences in Processing of Objects Versus Backgrounds

Comparisons of older adults also substantiate cultural differences in object, rather than background, processing (Goh et al., 2007). The study by Goh et al. relied on measures of neural adaptation, using a paradigm in which either the central object or the background component of a complex scene was repeated while the other component varied (or both were repeated as a control condition). Upon subsequent presentations of the same information, neural regions originally responsive to the information should show reduced activation. Because regions adapting to objects versus backgrounds can be separated with this approach (Goh et al., 2004), it is possible to independently compare the effects of culture on neural adaptation to objects and backgrounds. Whereas young adults across cultures exhibited similar patterns, older Singaporeans exhibited *reduced* adaptation to objects compared to older Americans, indicating less attention or sensitivity to objects. Background adaptation was relatively similar across cultures. Although this study did not directly assess memory per se, adaptation is relevant to memory in that it is an assay of previous experience with information. Follow-up studies indicate that the age-related changes across cultures in adaptation may be highly influenced by the intentional nature of the task. When older Singaporeans were instructed to attend to the objects, their neural adaptation matched the level of that of Americans (Goh et al., 2007). Thus, the age-related losses in adaptation may be selective depending on the person's orientation.

## Memory for Social Contexts

Although studies have typically focused on objects and backgrounds, they have also explored social and emotional stimuli. Koreans are better than Americans at recognizing background scenes presented behind emotional faces (Ko, Lee, Yoon, Kwon, & Mather, 2011). With age, there is a surprising reversal of the pattern such that older Americans better remember the background scenes compared to older Koreans. The authors suggest that this may reflect the fact that attending to the central face may be particularly demanding for older Koreans, who have repeatedly engaged in the cultural practice of attending to context. Thus, this central focus disproportionately impacts their memory for backgrounds.

Experiments have also investigated scenes consisting of entirely social stimuli, such as groups of individuals. When a central character is flanked by other secondary characters, Americans and Japanese differ in what they remember about the background characters. Whereas Japanese recognize changes in facial expressions (e.g., frowning to smiling) in background characters more than do Americans, the groups remember equivalent amounts of information about the central character (Masuda et al., 2008).

## Specificity of Memory

Another aspect of memory that may differ across cultures is the specificity of the remembered information. People tend to remember gist, schemas, and thematic information but not the specific details of information (Schacter, 1999). These tendencies are particularly pronounced with age (Koutstaal & Schacter, 1997) because fluid cognitive resources are reduced with age. Thus, comparing the specific details encoded into memory may be a particularly sensitive assay of cultural differences. Westerners adopt a feature analysis strategy that relies on detailed analysis of the parts, and they might therefore be expected to better remember perceptual details of an object. Recent studies have found support for this idea, such that Americans are better than East Asians at identifying which items tested at recognition were the exact same as the exemplars studied at encoding rather than merely similar (e.g., a second bicycle, but one with a different color or shape than the one originally studied) (Millar, Serbun, Vadalia, & Gutchess, 2013). In contrast, recognition at the item level, remembering whether or not a bicycle had been studied before (regardless of whether the perceptual details were identical), was equivalent across cultures. This tendency for Americans to better remember perceptual details extended to background scenes, suggesting that the effect was not simply limited to memory for objects or due to the use of decontextualized objects on a blank background.

## Source Memory

One potential interpretation of the original findings by Masuda and Nisbett (2001) is that East Asians are more sensitive to the binding or association of information together. That is, if the focal objects were more tightly associated with their backgrounds for East Asians, removing or changing the background would impair memory more than it would for Americans. Based on this logic, one might predict that East Asians should better remember associations of a variety of types compared to Americans. This hypothesis spurred work on other aspects of associations in memory, such as source memory. Source indicates from where information was learned (e.g., which person told you a new fact or piece of gossip). Thus far, we have focused on memory for items, a focal object or an aspect of the background, but it is also possible to assess memory for other properties of the information, such as the source. Compared with item memory, source memory is disproportionately impaired with age. Given that source can indicate the reliability of information (e.g., "Did I learn this health-relevant information from my doctor, or is it a dubious claim from an infomercial or uninformed friend?"), source can have important implications for the inferences that older adults should make about remembered information.

One study investigating source memory did not find the expected cultural difference (i.e., that associations would be better remembered by East Asians than Americans) (Chua, Chen, & Park, 2006). Younger and older Americans and Chinese learned facts presented in a video by one of four sources (a younger or older male or female; all sources were from the same culture as the participant). Although there were no effects of culture, age-related decline in source memory occurred equivalently across cultures. This result also converges with another aspect of the study of object–background adaptation discussed previously (Goh et al., 2007). The repetition of object–background pairs in that study induced adaptation in hippocampal regions associated with the binding of information together. Both Americans and Singaporeans evidenced a reduced adaptation response with age in these binding regions. Together, these results suggest that impairments in associative memory, including aspects such as source memory, may be universally impaired with age. Of course, tests across a broader variety of cultures than Americans and East Asians are needed to fully substantiate this claim.

Another study investigated the effect of culture for source memory using a paradigm in which older adults sometimes performed equivalently with young, perhaps as a result of the socioemotional relevance of the task (e.g., source indicates whether a person is good or evil). Whereas Canadian older adults did not perform worse than young on an item memory (old/new) test, older Chinese were more impaired than their young counterparts (Yang, Chen, Ng, & Fu, 2013). Source memory showed a similar pattern, although the worse performance of older Chinese did not reach significance. A second experiment addressed another aspect of source memory, testing whether an item had been perceived or imagined, and the results showed a similar pattern. Although the more pronounced effects of aging on source memory for Chinese participants diverged from the pattern of results from the study of source memory by Chua et al. (2006), Yang et al. characterize their tasks as assessing categorization (e.g., either good or bad; perceived or imagined). According to this explanation, the support provided by categories at encoding benefits older Americans more than older Chinese, consistent with their greater declines in memory and in contrast to previous studies of source memory that did not support categorical processing (Chua et al., 2006). This interpretation of Yang et al.'s data interfaces with the study of categorization and memory, which has been investigated across cultures in several studies.

## Categorization and Memory

Categorization has emerged as one of the most consistent areas of cross-cultural differences. These studies illustrate some cross-cultural differences in semantic memory, which is the subtype of memory considered to be the storehouse of the facts and knowledge acquired over one's lifetime. Several studies have focused on sorting tasks, asking participants to group items together and sometimes probing for explanations of groupings (Chiu, 1972; Ji, Zhang, & Nisbett, 2004; Unsworth, Sears, & Pexman, 2005). These studies found that whereas Westerners tended to sort information taxonomically, relying on categories and similar attributes, East Asians tended to use thematic categorization, emphasizing a variety of different types of functional relationships among items. For example, if presented with the triplet cow–grass–chicken and asked which two items go together, Americans and Canadians would tend to sort cow and chicken together, explaining that both belonged to the category "animals." Chinese, on the other hand, might sort cow and grass together, explaining that cows eat grass. These patterns appear to be robust, extending across multiple cultural groups and testing languages, (Ji et al., 2004).

Neurally, East Asians and Americans show substantial overlap in the networks engaged during the evaluation of categorical versus relational associations (Gutchess, Hedden, Ketay, Aron, & Gabrieli, 2010). When categorical and relational tasks were together compared against a control task, some cultural differences emerged in neural activation. The fact that the differences extended across both types of judgments suggested that there was conflict between the two types of judgments and that both cultures likely evaluated both types of relationships when making judgments. East Asians resolved the conflict by engaging attentional networks, denoted by frontoparietal activity, whereas Americans resolved the conflict by engaging regions related to semantic processes, such as temporal lobe regions. Although these results do not speak to cross-cultural differences in the types of knowledge stored in semantic memory, the data indicate potential cross-cultural differences in resolving conflict between competing types of representations.

Cultural differences in reliance on taxonomic versus thematic categorization have also been probed with long-term memory tasks. This topic is explored in one of the few studies of cultural differences in implicit memory—memory that does not require conscious awareness of accessing the past—in contrast to the overwhelming emphasis on explicit memory, or memory requiring conscious awareness (e.g., to identify something as "old" or "new"), in the cross-cultural literature. In this study, Westerners and East Asians were presented with primes that were associated with a target picture either categorically or relationally, such as through a functional connection (Unsworth et al., 2005). Participants had to decide as quickly as possible whether the prime word and the target picture were related, and reaction times were used as an implicit measure of the strength of the association, compared to a control condition. Whereas East Asians' reaction times were similarly fast regardless of whether the picture was primed with a categorical or relational item, Westerners' reaction times were faster with categorical primes. These results suggest that cultural differences could occur in semantic memory. The inference is that faster reaction times reflect direct connections, or fewer nodes, between concepts than when there are longer reaction times. Thus, the data suggest that East Asians may have associations between both relational and categorical knowledge, whereas Westerners have more selective categorical associations. Direct connections between concepts represent the more elaborated thinking style that develops with repeated engagement with cultural practices.

Cultural differences in the use of categories have also been tested in explicit long-term memory. Categories have long been recognized as a useful way of organizing and cueing the retrieval of information from memory. After learning a list of words presented in a random order, people tend to spontaneously cluster words by category as they retrieve them, perhaps listing all of the vegetables together in order before moving on to recall words from another category, such as animals (Bousfield, 1953). Words sharing categorical relationships also tend to be better recalled than words in an unrelated list because the categories can serve as retrieval cues to aid in remembering information. In a study assessing the use of this categorical clustering strategy across cultures, young and older adults from American and Chinese cultures recalled more words from a categorically related list than from an unrelated list (Gutchess, Yoon, et al., 2006). However, the use of a categorical clustering strategy differed across cultures. Whereas young Americans and Chinese similarly used the strategy, older Americans used a categorical clustering strategy more than older Chinese. This was thought to reflect the greater facility of using categorical memory strategies throughout one's lifetime for older Americans but not older Chinese. Whereas young adults have sufficient cognitive resources to adopt an optimal strategy that may be less familiar or well-practiced, limitations in cognitive resources may make this more difficult for older adults. In this case, Chinese older adults would encounter more difficulty applying the less familiar categorization strategy.

## False Memory

Our review thus far has focused on what information is differentially retained and emphasized in memory across cultures, such as whether memory is better memory for objects versus backgrounds and whether categories serve as useful retrieval cues. We argue that cultural differences in these details and strategies signify what a culture values. If the information was retained in memory or aided as a retrieval cue, this indicates that it was prioritized in information processing in place of other information. The study of memory errors may be a particularly rich domain in which to study cultural differences because distortions provide clues to how information is organized in memory. Memory errors likely reflect a purer contribution from the information and strategies that are salient, accessible, and well-practiced because these processes are not opposed by actual familiarity or recollection of information from memory.

In a recent study (Schwartz et al., 2014), we assessed cross-cultural differences in false memories for categorically related information. As discussed in the section on categorization, Americans tend to use categories to organize information in memory more than do East Asians, and this can influence the accurate recall of information for older adults (Gutchess, Yoon, et al., 2006). By assessing the impact of categorization on memory errors, we sought to identify whether a categorization strategy also made individuals more prone to commit memory errors. In a comparison of Americans with Turks, whose culture has been shaped by both Western and Eastern influences, we found that Americans committed more categorical memory errors when trying to recall word pairs. In contrast, Turks were more likely than Americans to mispair other words off the studied list (that were not related categorically). Whereas both groups correctly recalled similar amounts of accurate information, the type of memory errors varied across groups.

Although the study by Schwartz et al. (2014) relied on a simple laboratory paradigm using controlled presentation and testing of word pairs, false memories can be quite robust and shape individuals' reconstruction of life events. False memories can be as simple as confidently remembering a word that had not actually been read earlier; however, they can also emerge as detailed, but fabricated, autobiographical memories of personal events, such as being lost in a shopping mall as a child (Loftus, 2005). These false memories can be quite compelling, with words mistakenly recalled as having been presented in a list as much as 55% of the time for young adults (Roediger & McDermott, 1995) or resulting in detailed recountings of events that were never experienced (Loftus, 2005). Thus, it is important to understand potential cross-cultural differences in memory errors because diverging recollections of events could lead to misunderstandings between individuals or groups. It is easy to imagine a scenario in which two heads of state differ in their recollections of a critical interaction, with both quick to attribute negative motives to the other party rather than considering the contribution of faulty memory. Recall that on the campaign trail in 2008, Hillary Clinton famously recounted a story of running for cover from sniper fire after landing in Bosnia during her time as First Lady. Subsequent investigation revealed this to be a false memory. Political opponents were quick to cast aspersions on the basis of her false claim; such a misstatement at the international level could have more severe repercussions in the case of political enemies or uneasy allies, particularly when national pride is inflamed by the insult of being "lied to" or being cast as the subject of an unflattering false recollection.

## Self-Relevance and Memory

Although the literature reviewed thus far focuses largely on traditionally studied cognitive aspects of memory, evidence from studies conducted primarily with Westerners suggests that memory for socially relevant information may rely on different mechanisms than those supporting nonsocial memory. Distinct neural regions support memory for socially relevant information, such as information related to self or others; moreover, patients with profound amnesia and the inability to form new memories are able to exhibit memory for impressions about others (for review, see Kensinger & Gutchess, 2015). Because many cross-cultural differences in cognition (e.g., attention to field or context vs. categories) may result from differences in social processes (e.g., looking to the group or considering relationships between individuals), social memory may be particularly prone to effects of culture (for further discussion of this topic, see Huff, Ligouri, & Gutchess, 2014). Although there is a robust cross-cultural literature investigating differences in social processes, study of this topic is only beginning to interface with that of memory. Here, we review research at the interface of social processes and memory.

One of the most extensively studied topics in cultural psychology is the distinction between independent and interdependent self-construals, which has been described as conceptualizing of the self as an entity distinct from other persons (independent) or as tightly integrated with others (interdependent) (Markus & Kitayama, 1991). The most striking differences have been found between Westerners (i.e., Americans in the United States), who tend to value individuality and uniqueness, and Easterners (i.e., Japanese, Chinese, and Korean), who place more emphasis on relationships and connectedness. These styles of thinking about the self are pervasive and influence memory for self-relevant information (Sui et al., 2007; Wagar & Cohen, 2003; Zhu & Zhang, 2002). In addition, Wagar and Cohen have shown that self-construal influences successful encoding of long-term memories relevant to the personal (i.e., more independent aspect) and collective (i.e., more interdependent aspect) self. These researchers argue that measuring long-term memory serves to better understand stable cultural differences in self-construal.

Using long-term memory as a measure of cultural differences can access more stable, consistent traits, such as adherence to either the personal or the collective self (Wagar & Cohen, 2003). Repeated engagement with cultural practices emphasizes either independence or interdependence and thus contributes to the strength of the representation of the personal or the collective self (Kitayama, Markus, Matsumoto, & Norasakkunkit, 1997; Kitayama & Uskul, 2011; Morling, Kitayama, & Miyamoto, 2002). With repeated engagement with cultural practices of an independent culture, an individual may have a more elaborated personal self that would be more easily accessible, especially at deeper levels of processing, such as long-term memory. Wagar and Cohen tested this hypothesis by using the self-reference effect paradigm and focusing on the personal and collective self with Euro-Canadians and Euro-Americans. The self-reference effect is defined as an enhancement in memory for traits related to or descriptive of the self compared to other conditions, such as traits that are descriptive of others (e.g., friend and mother) or traits that are encoded with lower-level processing (e.g., structural and semantic) (Kuiper & Rogers, 1979; Rogers, Kuiper, & Kirker, 1977; Symons & Johnson, 1997). In addition to memory enhancement for self-relevant traits, Wagar and Cohen hypothesized that there should be quicker recognition (faster reaction time) for words descriptive of the more elaborated self-construal. In order to test their hypotheses about both memory enhancements for descriptors of the personal versus the collective self and decreased reaction time for the more elaborated self-construal, they employed a modified self-reference paradigm with three levels of processing, (1) self-reference (e.g., “Does this word describe you?”), (2) other-reference (e.g., “Does this word describe your best friend?”), and (3) structural (e.g., “Is the first letter a vowel?”). The words presented were traits representing either the personal self (e.g., happy and smart) or the collective self (e.g., friend, student, and colleague). In the recognition task, following a 40-min delay, European-Canadians, who were hypothesized to have a more elaborated personal self, responded quicker to words from the self-reference condition than the other-reference condition. Asian-Canadians, hypothesized to have a more elaborated collective self, showed no difference in reaction time during the recognition task for words in the self-reference or other-reference condition. In addition, there was an interaction between encoding condition (i.e., self, other, and structure) and trait type (i.e., personal and collective) in Asian-Canadians, such that reaction time was slower for personal trait words in the self-reference condition and quicker for words related to the collective self in the self-reference condition. This finding implied greater elaboration of the collective self in Asian-Canadians. An important finding from this study is that the differences only emerge at the time of recognition, or after the traits have been encoded in long-term memory. These findings indicate greater cultural differences at deeper levels of processing that engage the stable, more elaborated style of self-construal.

## Autobiographical Memory

Autobiographical memory is another type of long-term memory that tends to vary systematically as a function of cultural differences in self-construal. Moreover, because many autobiographical memories are interpersonal, an individual's memory of a past event provides a lens into his or her interpretation of the event and understanding of his or her position in relation to others. In order to foster the independent self-construal, individuals from Western cultures may place emphasis on a detailed image of the self in past events, whereas individuals from Eastern cultures may concentrate on the self as a member of interpersonal interactions and view themselves in relation to others, thus fostering the interdependent self-construal (Nelson & Fivush, 2004). Research on autobiographical memory has provided support for this claim. When asked to recall past events, American adults focus on their role and feelings within specific, discrete personal events. Alternatively, Chinese individuals recall more social and historical events and tend to focus on their connectedness with others (Wang & Conway, 2004). These cultural differences in autobiographical memory promote the development of either an independent or an interdependent self-construal (Wang & Conway, 2004). This developmental process may start with very early autobiographical memories, which reportedly occur earlier for European American children than for East Asians, consistent with the Western notion of the self as more autonomous and independent (Peterson, Wang, & Hou, 2009; Wang, 2006). In addition to reporting having earlier memories, European Americans also impart autobiographical memories that are more detailed and specific compared to those of East Asians (Jobson & O'Kearney, 2008; Wang, 2001, 2004).

One important factor that contributes to cultural differences in autobiographical memory is differences in parenting. Western children are encouraged to discuss their feelings and thoughts after an event, and Eastern children are more frequently told how they should feel or interpret an event (Ross & Wang, 2010). In an Eastern context, parents encourage children to think about their role within the situation and context. In the Western style of parenting, children are encouraged to think about their individual role in an event and how it separates them from others or highlights their uniqueness. When children are asked to discuss personal experiences, European American children place emphasis on their feelings, preferences, and opinions, whereas East Asian children focus on social interactions and provide less detail (Ross & Wang, 2010). As evidenced from research with American and Chinese children, these early interactions with parents seem to profoundly impact how children recall information from the past. As previously discussed, long-term memories seem to be linked to the more stable, consistent aspects of self-construal that have been developed by repeated exposure to cultural practices and parenting style that promote the continuation of cultural norms. Although research on long-term memory provides insight into the development and maintenance of self-construal, recent investigations have also incorporated the study of neural mechanisms to understand cultural differences in self-construal. One justification for this new line of investigation was posed by Kitayama and Uskul (2011), who suggest that repeated engagement in cultural practices shapes neural connections. Recent evidence in cultural neuroscience supports the hypothesis that culture is "embrained." In the next section, we discuss emerging work on neural substrates underlying long-term memory that may differ across cultures.

## Neural Underpinnings of Self-Relevant and Autobiographical Memory

Before delving into a discussion of the neural underpinnings of long-term or autobiographical memory, it is important to revisit the self-reference effect paradigm in order to understand how self-relevant information is processed in the brain. Numerous neuroimaging studies have found increased activation in the medial prefrontal cortex (mPFC) and posterior cingulate cortex (PCC) when participants judge information relevant to the self, as contrasted against judging information relevant to others (Craik et al., 1998; Gutchess, Kensinger, & Schacter, 2007, 2010; Han & Northoff, 2009; Heatherton, Macrae, & Kelley, 2004; Heatherton et al., 2006; Kelley et al., 2002; Macrae et al., 2004; Northoff, Heinzel, de Greck, Bermpohl, & Dobrowolny, 2006). Concurrent activation in these two regions has provided evidence for a network, known as the self-referential network, that is distinctively involved when processing information relevant to the self (see Chapter 13).

Evidence from cross-cultural investigations in China suggests that activation of the self-referential network may be modified by cultural differences in self-construal, as assessed with functional magnetic resonance imaging (fMRI). While judging whether traits describe the self, participants from both Western and Chinese cultures engaged the self-referential network (mPFC and PCC). Interestingly, Chinese, but not Western, participants also engaged this network while making judgments about the mother (Zhang et al., 2006; Zhu, Zhang, Fan, & Han, 2007). The authors argue that the interdependent self-construal that is more pervasive in East Asian cultures encourages individuals to include close others in their representation of the self; the overlap in neural regions that support the processing of information relevant to the self and close others provides further evidence for this interconnectedness (see Chapter 13). On the other hand, the independent self-construal that is more common in Western cultures encourages individuality, uniqueness, and separation of the self from others; therefore, processing information relevant to the self engages a distinct network from processing information relevant to others (Zhu et al., 2007).

Consistent with the findings for self-relevant processing in Western and Chinese participants, evidence suggests that self-construal modifies the self-reference effect in memory as well. Both Chinese and Western participants demonstrate memory enhancements for self-relevant information. However, Chinese participants also exhibit improved recognition for mother-relevant information (Zhang et al., 2006; Zhu & Zhang, 2002; Zhu, et al., 2007). These findings bolster the hypothesis that Easterners include close others in the representation of the self.

One component of self-referential processing that was previously overlooked in neuroimaging research is that of the social self, as illustrated in the behavioral work of Wagar and Cohen (2003). The social self is especially relevant for those with an interdependent self-construal because they derive their identities from relationships and a feeling of interconnectedness. In many of the studies reviewed previously, the traits individuals processed and later recognized were exclusively personality traits (e.g., “smart” or “funny”). In a recent investigation, Ma and colleagues (2014; for a detailed description of this study, see Chapter 13) attempted to improve upon this design by examining three dimensions of trait judgment (personality traits, physical traits, and social roles/identities) in Danish and Chinese participants. The results showed that those high in interdependence were more likely to engage the temporoparietal junction (TPJ), a region associated with thinking about the mental states of others (Jenkins & Mitchell, 2010; Lombardo et al., 2010; Saxe & Kanwisher, 2003), and less likely to engage the mPFC while reflecting on social attributes (vs. personality or physical attributes) relevant to the self. Other researchers in Korea performed a similar study measuring the effects of individual differences in self-construal on the self-reference effect for personal versus social information. Neural findings were in agreement with those of Ma et al. in that Koreans showed increased activation in mPFC while judging self-relevant personality traits and increased activation in TPJ while making judgments about self-relevant social information. In addition, these researchers found that cultural orientation moderated the self-reference effect such that those who were more independent (individualistic) showed greater memory enhancement for personality traits, whereas those who were more interdependent (collectivist) experienced greater memory enhancement for social traits (Sul, Choi, & Kang, 2012). As discussed in further detail later, an important next direction for the investigation of cultural differences in the personal and collective self would be to use neuroimaging to understand the neural regions that support *memory* for self and social information across cultures. Many researchers have examined behavioral measures of self- and other-relevant memory across cultures (Sul et al., 2012; Zhu et al., 2007), but to date, there have been no investigations of the neural regions specifically supporting memory for this information.

## Priming Cultural Orientation

In order to further understand cultural differences in self-construal and self- and other-relevant memory, experimental manipulations such as priming have been employed. We previously mentioned that although individuals possess a chronic tendency to hold an independent or interdependent self-construal, they are also likely to possess aspects of both personal (independent) and collective (interdependent) self-construals. Thus, the way people think about the self can vary depending on the situational context. Priming can be employed to temporarily orient individuals toward one of these self-construal styles and potentially moderate memory and neural activations during self- and other-relevant judgments (Gutchess & Indeck, 2009). In an fMRI study by Chiao and colleagues (2010), participants were primed with either independence or interdependence prior to completing a self-judgment task that employed two types of personality trait judgments: general and contextual. The researchers hypothesized that those exposed to the independence prime would show greater activation in the self-referential network (mPFC and PCC) for general traits, whereas those exposed to the interdependence prime would show greater activation for context-specific traits. In support of these hypotheses, researchers found that priming caused differential neural responses by enhancing activation in the culturally congruent condition. Other research from the same lab found that cultural priming modulates neural activity in the dorsal region of the mPFC when making judgments related to the self, close others, and unfamiliar others (Harada, Li, & Chiao, 2010). Researchers in Hong Kong have found consistent evidence of distinct neural activation between self and close others following a Western (independent) prime and little or no distinction between self and close other following an Eastern (interdependent) prime (Ng et al., 2010). Although current research using cultural priming has been important in attributing causality through the random assignment of participants to culturally laden self-construal groups using priming, this approach has not been used to study memory.

In order to understand how repeated engagement with cultural practices influences long-term, stable traits associated with the self, as discussed by Wagar and Cohen (2003), it would be necessary to measure neural activity using deeper processing than quick trait judgments. Studies of long-term or autobiographical memory may allow for this, especially following a cultural prime. Research with Western participants shows that the self-referential network (e.g., mPFC and PCC) implicated in judgments of the self also supports successful *encoding* of self-relevant information into memory (Kelley et al., 2002; Macrae et al., 2004). One might expect that the same cultural differences observed in processing for information relevant to the self versus others would extend to subsequent memory, but there is a dearth of research in this area, especially that incorporates cultural priming. A similar gap in the literature exists for autobiographical memory in that there is some neuroimaging research with Western populations that has identified areas underlying autobiographical memory, but this has not extended to other populations. Research with Western participants suggests that autobiographical memory is supported by a left lateralized network that includes the prefrontal, medial, lateral temporal, and cingulate cortex, in addition to the TPJ and the cerebellum (Martinelli, Sperduti, & Piolino, 2013; Svoboda, McKinnon, & Levine, 2006; for review, see Cabeza & St. Jacques, 2007). Incorporating the study of cross-cultural differences into this line of research would be beneficial for further understanding the mechanisms of deeper-level processing of the self. It is possible that cultural differences would be even larger when measuring long-term and autobiographical memory than what is seen in the studies of trait judgments because these processes should access a more stable and elaborated self-construal.

## Emotional Memory

Whereas we previously reviewed some studies (e.g., Ko et al., 2011; Masuda et al., 2008) assessing memory for emotional information, in this section we focus on the effect of aging on emotional memory and discuss the influence of culture. A finding that has received much attention in the aging literature is that of motivational shifts that occur with age. Whereas young adults tend to prioritize and be motivated by the acquisition of novel information, awareness of limited time remaining in one's life leads older adults to undergo a shift in motivation such that they prioritize spending time with close others (Carstensen, Isaacowitz, & Charles, 1999). This socioemotional selectivity theory also suggests that older adults should better regulate their emotions and preferentially attend to positive emotional experiences. This positivity shift is in contrast to young adults' prioritization of negative emotional information, which is thought to convey an evolutionary benefit through heightened attention to threats in one's environment. These motivational shifts with age also impact cognition and memory. Older adults exhibit a "positivity bias" such that they better remember positive than negative information (Mather & Carstensen, 2005) or, more commonly, show equivalent memory for positive and negative information, in contrast to young adults' better memory for negative information (Murphy & Isaacowitz, 2008).

Testing the existence of a positivity bias across cultures could be interesting for many reasons. The bias was originally proposed to reflect awareness of the limited time remaining in one's life, which suggests that the positivity bias should emerge with age across cultures, regardless of life experiences. However, it is also possible that prioritization of different types of emotional experiences across cultures could impact the emergence of a positivity bias. For example, cultures differ in their levels of dispositional optimism. Whereas older Americans tend to show more dispositional optimism than young, Hong Kong older adults have less dispositional optimism compared to young, reflecting the values that are emphasized within each culture (You, Fung, & Isaacowitz, 2009). Thus, the positivity bias could reflect the types of emotional experiences that are encouraged or prioritized in a culture.

It is also possible that positivity biases are shaped by the trajectory of a culture over time. For example, unique cultural histories of traumatic events (e.g., war, genocide, and poverty) or current unstable political regimes could impact the emphasis on positive emotions with age. Although collective memory, the ways in which groups may remember or repress culturally important events, has received substantial consideration in fields including politics, literature, and anthropology (see Assmann & Shortt, 2012), it has only begun to be investigated in psychological empirical research (e.g., Rajaram, 2011). This should be a rich area for future cross-cultural research addressing the ways in which individuals remember information together, even for relatively simple laboratory-based events.

Generally, the positivity bias in memory with age seems to emerge across both Eastern and Western cultures, although there are exceptions. Korean older adults better recognized positive over negative pictures and tended to recall similar amounts of positive and negative pictures (Kwon, Scheibe, Samanez-Larkin, Tsai, & Carstensen, 2009). This pattern was in contrast to young adults' better recall and recognition of negative pictures compared to positive ones. Likewise, young adults in Korea and the United States better recognized negative background pictures, whereas this negativity bias was reduced with age across cultures (Ko et al., 2011). Older adults in China (Chung & Lin, 2010) and Hong Kong (Fung, Isaacowitz, Lu, & Li, 2010) also exhibit a positivity bias in memory recall, relative to younger adults. Although it could be expected that cultural differences in expectations and views of aging might impact the extent to which older adults show a positivity bias, support has not been found for these ideas. Although older adults hold more positive views of aging in China than in the United States, these views are unrelated to the positivity bias in memory (Chung & Lin, 2012).

One exception to the finding of a positivity bias across cultures with age occurred with samples from Hong Kong. Whereas American older adults tend to look toward positive stimuli relatively more than young (Isaacowitz, Wadlinger, Goren, & Wilson, 2006), Hong Kong older adults look away from positively valenced stimuli (Fung et al., 2008). Although this study did not include memory measures, a number of other study designs or sample features could account for the different findings across studies. One factor to be investigated in subsequent research focused on the role of self-construal. Results suggest that the extent to which an individual considers him- or herself independent versus interdependent could influence the presence and magnitude of a positivity bias with age (Fung et al., 2010). Because Hong Kong has a number of Western influences, it is possible that samples drawn from the region across different studies could diverge from each other on this dimension.

## Conclusions and Future Directions

In this chapter, we reviewed a number of studies on the effects of culture on memory, noting differences in processes across cultures. Specifically, Eastern and Western cultures differ in their memory for focal objects versus backgrounds, the use of categories in memory, and information relevant to the self. Many similarities across cultures are also noted; for example, with aging, source memory tends to decline and positive information is prioritized in memory. However, the literature on memory across cultures is sparse, with at best only a few studies investigating any given topic. Studies interfacing with other literatures and methods are sorely needed. For example, although many studies have investigated cultural differences in self-construal, few of these investigated the impact on memory or the neural regions involved in encoding, storing, and retrieving information in memory. Applying a cognitive neuroscience lens to these questions is important for further delineating the processes that differ across cultures. Such an approach has the potential to provide solutions to how to support more effective memory processes. For example, which stage of memory processing differs across cultures, leaving some individuals more prone to certain types of distortions and inaccuracies in memory?

Such questions are particularly important for the study of aging because globally we face the challenges associated with aging populations. Medical innovations are allowing for the elongation of life, but this does not guarantee that individuals will remain healthy. Particularly in countries such as China, the number of older adults will rapidly outpace the number of younger adults due to low birth rates. The economic and healthcare burden of supporting an aging society is not trivial. Understanding how to better support intact cognition and memory with age is important in prolonging the period during which older adults can live independently and maintain adequate function to perform essential activities of daily living (e.g., remembering to take medications according to a daily schedule). Although there is considerable variability in the abilities of older individuals within a culture, with some maintaining cognitive function considerably better than others, culture can be thought of as one more individual difference factor, such as working memory span or personality type, that can be useful in predicting the likelihood of different outcomes with aging.

Comparing across cultures can allow us to identify which cognitive functions are universally impacted by aging as well as those for which a particular cultural lens may impart strategies and information processing biases that serve a protective function for cognition with age. For example, is self-relevant processing a more effective memory strategy for Western than Eastern older adults, as a result of processing of the self as a unique entity throughout life? Although Western older adults exhibit overly general memory (Koutstaal & Schacter, 1997), does the relatively better memory for perceptual details in young adulthood allow them to better adopt strategies to encode more accurate and detailed memories than Easterners with age? Or despite the initial advantage for Westerners in young adulthood (Millar et al., 2013), is there a steeper rate of decline in memory for details in Westerners than Easterners across the lifespan?

It is important to study both the universality of age-related changes and cultural differences in trajectories of age-related change because they may help to identify remediative strategies and inform the creation of training programs through which individuals may be able to improve memory function through instruction in specific strategies and application of them to daily life. Here, we focused on the interplay between cognitive resources and culture, but it is important to note that cohort effects also impact comparisons between age groups. Although this can be a challenge in that cultural change may occur across generations, we argue that comparing cultures across different generations can make a distinct contribution. Comparing multiple cohorts can distinguish differences truly due to culture, based on nationality or other more stable facets of group identity, from the influence of specific one-moment-in-time events that disproportionately influence a single cohort in one culture, such as the Great Depression or the Cultural Revolution. Identifying stable patterns of differences across different cohorts provides confidence that it is the enduring factors of culture that exert enduring influences on behavior (for further discussion, see Gutchess & Goh, 2013).

In terms of public health, memory across cultures is relevant in considering the trajectory of abnormal aging processes in disorders such as Alzheimer's disease (AD). Within the United States, some data indicate racial and ethnic disparities in AD affecting widespread factors such as the incidence, diagnosis, trajectory, and treatment of the disease. For example, some data indicate that African Americans and Americans of Hispanic origin have higher prevalence of dementia than non-Hispanic whites (as reviewed by Chin, Negash, & Hamilton, 2011). In addition to potential differences in biological factors, such as genetic risk factors, many cultural factors seem to impact the course of treatment and outcomes (Chin et al., 2011). For instance, some cultural groups consider the symptoms of AD, such as profound memory loss, to be a normal effect of aging and so may be less likely to seek treatment. Groups can differ in their comfort with the medical community, and research and treatment recommendations may not take into account the unique needs and challenges of different groups. For example, the mental health needs of Asian Americans may not be recognized because they are often viewed as a successful "model minority" such that the influence of acculturative stress and discrimination often go unrecognized (Hall & Yee, 2012). Even when individuals do consult medical professionals, available providers may not be culturally competent (Hall & Yee, 2012) and bias may influence treatment. For example, minorities are prescribed medications intended to slow the progression of memory impairment less often than whites (as discussed by Chin et al., 2011). Culture may also impact caregivers' conceptions of AD compared to "normal aging." The stigma surrounding AD could affect how likely caregivers are to seek treatment for a loved one or even their willingness to seek social support for themselves; Asian Americans may be particularly impacted by the stigma of AD (Liu, Hinton, Tran, Hinton, & Barker, 2008). Currently, there is very little experimental work investigating the impact of AD across cultural groups or evaluating the potential efficacy of different memory strategies or treatments to alter the trajectory of the disease. This gap could be one where the study of cross-cultural differences in memory has strong applications to begin to understand and address health disparities.

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## CHAPTER 11

# When Culture Informs Neuroscience: Considerations for Community-Based Neurogenetics Research and Clinical Care in a First Nation Community With Early Onset Familial Alzheimer Disease

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### Abstract

The meaningful consideration of cultural practices, values, and beliefs is recognized as a significant factor for the effective translation of innovation in neuroscience to clinical practice. Given increasing attention to the cultural diversity of society and the immense investment in the biomedical sciences, it is essential to study how potential discoveries in neurodegenerative diseases, such as Alzheimer disease, are perceived and utilized across cultures. Key questions about culture interact with issues surrounding the acceptance of disease-related cognitive decline and personality changes, possibilities for predicting disease, and methods of intervention. The unique circumstances described in this chapter highlight the complexities of cultural considerations in research and the significance of cultural neuroscience as an emerging field.

**Key Words:** neurogenetics, First Nation community, Alzheimer disease, culture, diversity

## Introduction

Research in cultural neuroscience is premised on understanding how the brain and its neurobiological mechanisms shape and facilitate the transmission of culture, as well as how cultural traits (e.g., belief systems, practices, and values) shape neurobiology (Chiao et al., 2010). Our research is rooted in the latter of these topics, specifically in investigating how different cultures inform and broaden understandings of the brain beyond a Western biomedical model. What role does culture play in coping with a genetic form of neurodegenerative disease? How do cultural traits influence understandings of sickness, brain health, and care? What is the significance of conducting culturally relevant research, and how will it allow us to approach cultural neuroscience in a more ethical and comprehensive way?

In an interdisciplinary effort bridging the clinical neurosciences, ethics, and clinical services, we are engaged in community-based research with a Canadian First Nation population, in which a large family carries a presenilin-1 (*PS1*) gene mutation leading to early onset familial Alzheimer disease (EOFAD). Our primary research goal is to explore the intersections of Western knowledge, traditional teachings, and culturally specific understandings about EOFAD. Through the evolution of this work, a number of pragmatic and conceptual ethical considerations have emerged. This chapter explores how culturally oriented work in neuroscience raises unique challenges that both complicate and expand traditional Western biomedical approaches to research and analysis. We begin by discussing the integral but complicated emphasis on community when considering questions of confidentiality and informed consent in First Nations community-based research. Next, we discuss the role and conceptualization of family existing in many First Nation populations and how this understanding challenges traditional models of neurogenetics while concurrently expanding the possibilities for diverse and culturally responsive results. Finally, we elucidate the vexing challenge of managing incidental findings in community-based research with a First Nation population that is located both remotely and dispersed throughout various regions of the country. The unique circumstances described here highlight the complexities of cultural considerations in research and the significance of cultural neuroscience as an emerging field. Furthermore, in drawing attention to the ethical challenges, potential solutions, and imperative role of community-based health research in cultural neuroscience, we make the case for expanding the field to include research practices centered within communities as a necessary component to any neuroscience that seeks to understand, explain, and interpret the experiences of diverse cultures.

## Background

Between 1998 and 2009, nine members of a First Nations kindred were referred to the University of British Columbia Hospital Clinic for Alzheimer Disease and Related Disorders (UBCH-CARD) for medical assessment in the context of a strong family history of early onset dementia (Butler, Dwosh, et al., 2010). The family originates from a remote rural community, with members dispersed throughout British Columbia, the Yukon, and Alberta, Canada. Seven of the nine individuals received clinical diagnoses of possible or probable Alzheimer disease (AD). Genetic testing initiated on an affected family member in 2006 identified a novel *PS1* gene mutation, thereby confirming a diagnosis of EOFAD (Butler, Beattie, et al., 2010). Review of the family history identified more than 100 family members in direct lineage of affected individuals and at risk of inheriting this condition (Butler, Dwosh, et al., 2010).

Dementia has been identified as a major global health priority and is the most common neurodegenerative disease in adults (Wortmann, 2012). It is estimated that more than 35 million people live with dementia, which is anticipated to double by 2050 (Brookmeyer, Johnson, Ziegler-Graham, & Arrighi, 2007). Dementia, the umbrella term for cognitive decline that includes late-onset and early- onset AD, results in impaired memory, thinking, behavior, and ability to perform everyday tasks (American Alzheimer's Association, 2013). It significantly impacts individuals living with the disease, their family and caregivers, and broader communities. Early-onset AD accounts for approximately 5% of AD cases, and is characterized by the presence of symptoms prior to age 60–65. Pathogenic mutations in the PS1 gene (including the mutation found within this First Nation family) are inherited in an autosomal dominant fashion and demonstrate complete penetrance; children of affected individuals have a 50% likelihood of inheriting the disease-causing PS1 mutation and subsequently developing EOFAD (Butler, Beattie, et al., 2010).

The identification of a *PS1* mutation in this family raised concerns regarding dissemination of information and provision of clinical services (including neurological and neuropsychological assessments and also genetic counseling,) given constraints posed by geography and funding and introduced potential research and educational opportunities. Through a family day event organized at UBCH-CARD and a health fair held in the Nation's territories in 2009, the Nation signaled its desire to pursue further exploration about the disease and embarked on a collaborative endeavor with the UBC National Core for Neuroethics and UBCH-CARD.

The methodological and conceptual framework for this project is community-based research, guided by an indigenous approach (Wilson, 2008). The approach relies on an infrastructure that includes a community advisory group made up of key members of the Nation's governance and leadership, a community-based researcher whose role is to actively facilitate research between the Nation and the UBC team, and community liaisons who assist in the recruitment and organization of focus groups and interviews in the given territories. Every step of the research is filtered through and ushered by the continuous and dynamic interaction of the UBC team and these key representatives of the Nation. The primary data for this project are cultural concepts and understandings of wellness and dementia, collected through focus groups and interviews with members of the Nation.

## Confidentiality and the Role of Community in First Nations Health Research

As we describe in Stevenson et al. (2013), an indigenous community plays a unique and integral role in ensuring that its members are protected throughout the research process. The First Nations' concerns regarding community confidentiality in this study were captured early in the research process and reflected in the research agreement signed between the Nation and UBC. The primary issues identified were the possibility of stigma and stereotyping of individuals, families, and the community and potential discrimination from employers and insurance companies. The research agreement ensures that every effort is made to maintain the anonymity of the Nation in any publications or presentations of the research endeavor and findings. All parties have agreed to revisit confidentiality throughout various stages of the research project. It currently remains in place for the ongoing protection of the community. In engaging the community from the inception of the potential project, and collaboratively formulating a mutually beneficial research agreement, researchers and participants were able to negotiate a culturally relevant approach that positioned the community as a fundamental partner in all steps of the process.[1]

Confidentiality in health research is traditionally focused on protections for individuals with the patient/research participant at the center of ethical and privacy concerns (Kleinman, Baylis, Rodgers, & Singer, 1997). The individually oriented basis for research ethics is highlighted in frameworks such as the *The Belmont Report*, which identifies "respect for persons, beneficence and justice" as the basic ethical principles guiding research on human participants (U.S. Department of Health and Human Services, 1979). Genetics research has broadened the scope of the individual protections because genetic information includes not only the individual but also the entire family (Lucassen & Parker, 2003). Different still is the role that protections play in community-based research involving culturally identifiable populations, such as indigenous communities. The requirements to protect an entire community challenge the traditional limits of confidentiality beyond solely their individual or familial focus.

The need for community-wide protections in indigenous health research come amidst a long history of oppression, colonization, unequal access to healthcare, and poor research practices. Critics of research conducted in indigenous communities have identified patterns of cultural insensitivity, lack of community involvement, stigma stemming from dissemination of results, lack of feedback during the research process, and exploitation of communities for academic or commercial gains as just a few of the concerns that have plagued this research (Brant Castellano, 2004; Wilson, 2008). An explicit misconduct of research with indigenous peoples was demonstrated when blood destined for rheumatic disease research from the Nuu-chah-nulth First Nation in British Columbia was instead used to investigate ancestry and population genetics without the First Nation's knowledge or consent (Arbour & Cook, 2006). The recent uncovering of ethically fraught nutritional experiments performed on Aboriginal children in Canada's residential schools between 1942 and 1952 depicts yet another sad chapter of poor research practice with indigenous peoples in Canada's history (Mosby, 2013).

Research policies and guidelines, primarily within Canada and Australia, have been adapted to capture the ethical issues raised by the participation of indigenous communities in human subjects research. Canada's *Tri-Council Policy Statement 2* (*TCPS2*) on "Research Involving the First Nations, Inuit and Métis Peoples of Canada," for example, seeks to broaden the scope of "concern for welfare" and requires, "consideration of participants and . . . their physical, social, economic, and cultural environments, where applicable, as well as concern for the community to which participants belong" (Government of Canada, 2010). The *TCPS2* and similar policy statements, such as those from the Canadian Institutes of Health Research in Canada and the National Health and Medical Research Council in Australia, acknowledge the important role that indigenous communities play in protecting the collective rights, interests, and responsibilities that also serve the individual rights of community members (Australian Government, 2006; Government of Canada, 2005).

Furthermore, a number of research principals, or codes of conduct, have been developed to ensure that work with indigenous populations is done in an ethical and "good way" (Ball & Janyst, 2008). The principles of "OCAP" are fundamental

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[1] As of January 2015, our research agreement with the Tahltan First Nation has been readdressed and confidentiality lifted. The issues discussed in this chapter refer to the research agreement and research implications prior to the change. Our important work with the Nation continues with this new openness today.

to conducting research with indigenous peoples in Canada, ensuring that indigenous populations maintain ownership, control, access, and possession of various or all aspects of research within their communities (First Nations Centre, 2007). Other notions of security and inclusion include the guiding principles of "protection, participation, and partnership" (University of Victoria, Faculty of Human and Social Development, 2003), and "the four R's of Aboriginal health": respect, relevance, reciprocity, and responsibility (Kirkness & Barnhardt, 1991).

Although these principals, protocols, and guidelines certainly ensure a greater degree of community protection in indigenous research, community-wide confidentiality remains a complex issue, especially in relation to codes of research conduct that emphasize individual protections and autonomy. Flicker, Travers, Guta, McDonald, and Meagher (2007) suggested that traditional research approaches may continue to stigmatize marginalized and vulnerable populations, instead calling for community-based participatory research (CBPR). They assert that CBPR may serve as an "effective new research paradigm that attempts to make research a more inclusive and democratic process by fostering the development of partnerships between communities and academics to address community-relevant research priorities" (Flicker et al., 2007, p. 478). These authors are careful to highlight, however, that this form of community-based research still faces significant ethical challenges because ethical review forms and guidelines remain focused on individual protections and often fail to account for common community-based research experiences.

Through the evolution of our community-based research investigating a remote and dispersed First Nation's experience with EOFAD, we have encountered a number of practical and conceptual challenges in enacting and maintaining the highest degree of community-wide confidentiality and protections. Although protection of the entire community is the basis of maintaining the Nation's anonymity throughout research, there remain competing interests between the imperatives to guard against possible stigma associated with the disease and the desire of community members to champion research from an indigenous perspective in a manner that fosters self-determination and ownership of research. Furthermore, community-wide confidentiality (especially when working with a geographically remote and widely dispersed population) challenges comprehensive outreach, recruitment, and dissemination of research findings. These issues are discussed briefly in order to highlight the nuances of culturally oriented neuroscience and the manner in which this work broadens and complicates traditional notions of neurological research and protections, such as issues of confidentiality. Such concerns elucidate the requirements for the active engagement of community in cultural neuroscience research in order to overcome challenging ethical implications for which existing policies and guidelines simply cannot account.

### Autonomy Versus Anonymity

Despite the overriding pressure to retain the anonymity of the Nation, some individual community members have signaled their discontent in not having the community named (Brief, 2010; Stevenson et al., 2013). These concerns arise over issues of self-determination and autonomy, especially in the face of a history of subjugation within poor research practice. Article 3 of the *United Nations Declaration on the Rights of Indigenous Peoples* states, "Indigenous peoples have the right to self-determination. By virtue of that right they freely determine their political status and freely pursue their economic, social, and cultural development" (United Nations General Assembly, 2007, p. 4). Furthermore, indigenous peoples in Canada have constitutional protections of their right to maintain their identity and participate as collectives in Canadian society (Brant Castellano, 2004). The principles of OCAP support these rights within research, ensuring that research is shaped by and representative of the Aboriginal populations involved (First Nations Centre, 2007; Schnarch, 2004). Although the principles of OCAP are integral to conducting research with indigenous peoples and can even be understood as "self-determination applied to research" (Schnarch, 2004), the protections and autonomy that these principles instill may be challenged or complicated by the application of community-wide confidentiality. Does community anonymity undercut a First Nation's autonomy in, and control over, research? How can individual autonomy be accounted for in this scenario? Writing for the First Nations Centre at the National Aboriginal Health Organization, Schnarch (2004) states that "OCAP is not a doctrine or a prescription. It is a set of principles in evolution" (p. 81) and therefore must be applied in conjunction with the best interests of the community. Whereas guiding principles in research tend to focus on individual protections, rights, and autonomy, the principles of OCAP often serve the indigenous community as a collective, ensuring that the community has control over research in a manner that is most suitable to the community requirements.

These tensions between autonomy and community anonymity emphasize the requirements for strong partnerships and a clearly defined research agreement prior to the commencement of research. Weijer (1999) reiterates the significance of a nuanced understanding of culture and community as he states, "Autonomous communities have their own politics, beliefs, and values and research may affect any of these elements" (p. 503). Open dialogue and deliberation on the benefits and harms of community-wide confidentiality are essential both to ensure adequate protections and to foster self-determination through the evolving and adaptable principals of OCAP. Attention to and understanding of culture and the imperative role of a cultural community in the evolution of the research process are fundamental to conducting cultural research in neuroscience and for ensuring that research is both inclusive and culturally relevant.

## Confidentiality and Knowledge Transfer

Given the geographic distribution of this First Nation population, comprehensive outreach and dissemination of progress and results is a continuous obstacle requiring strategic initiatives. The Nation's traditional territories are remote, with individuals living in rural, northern communities and dispersed throughout various regions of the surrounding cities and provinces. Traditional academic communications are often inadequate for keeping even urban-based communities up-to-date on research findings, let alone remote and dispersed communities for which access to follow up is especially challenging. The issue of results not being returned to the community, or returned in inaccessible language, has been identified by many indigenous Nations as a significant grievance regarding research conducted in their communities (Schnarch, 2004). Strategic, innovative, and creative methods must be embraced to find solutions to these tensions that are grounded in technological, geographic, and social forces.

Alongside the knowledge transfer enabled by community-based researchers and liaisons, the Internet can be a useful tool for widespread communication and for overcoming the logistics of geography. It is not without limitation, however, and breaches of confidentiality due to open access and unregulated networking are a fundamental concern. Research updates, community-based job postings, and recruitment letters posted online all have the potential to link researchers, individuals, and communities unexpectedly and openly to the sensitive research done within the community. The problem is double-edged: Specific information enables specific recruitment and tailored dissemination of information, but it places confidentiality at risk; generalized postings protect confidentiality, but their effectiveness in recruiting and providing meaningful updates is diminished and limited. In discussing the requirements for "authentic relationships as a precursor to ethical research" with indigenous communities, Bull (2010) emphasizes how "communities and researchers collaborate together in a co-learning environment, whereby mutual interests and agendas are discussed and enacted throughout the entire research process" (p. 13). Through our own research process, logistical communication issues are worked through and overcome by collaboration with a strong community advisory group and community research partners. Successful and ethical research would not be possible if it were not for this environment of co-learning, in which the interests and concerns of both parties can be openly discussed and collaboratively addressed.

Researchers cannot take for granted the challenges of knowledge dissemination when engaged in culturally oriented neuroscience research. Different communities may present different ethical implications regarding knowledge dissemination and community protections, and collaborative engagement with a given community allows for pathways to solutions that are ethically responsible, mutually beneficial, and agreeable.

## EOFAD and Concepts of Family: Bridging Biological and Cultural Understanding

The genetic prediction and diagnosis of EOFAD in this First Nation community highlights the relationships between core concepts of biomedical research and cultural beliefs and practices. Western scientific research necessitates a conventional approach to neurogenetics by exploring biological family lineage to map the history and scope of genetically caused disease. This emphasis creates unique tensions between biological and cultural conceptions of family. There is great diversity among First Nation families in Canada, but the ideal of a family unit is a large, extensive network of both biological family members and the broader community (Castellano, 2002). Indigenous communities hold distinctive views about relatedness and have familial expectations that inform everyday experiences of family (Bennett & Blackstock, 2002).

Of particular ethical relevance to genetic research, which requires adherence to the biological definition of family, is how social definitions of family may continue to be honored and upheld through research with indigenous peoples. Whereas biological lineage is central to determining genetic risk (i.e., inheritance of a PS1 mutation leads to EOFAD), how does the primacy of a strict biological definition of family impact cultural sense of identity and social structures that support EOFAD care and understanding? Our study has been well positioned to illuminate certain facets of culturally competent research in genetics, particularly the critical need to understand and respect principles of culture and social structure through consultation, education, continuous communication, and community verification throughout the research process (Arbor & Cook, 2006). Ultimately, we find that cultural definitions of family present opportunity for novel approaches to data collection and analysis in diverse communities. Furthermore, honoring and emphasizing the significance of beliefs and social structures within these communities allow for an ethical and nuanced approach to cultural neuroscience.

## All My Relations: Considering Complex Ideas of Family in First Nation Genetic Research

Genetics research is inherently tied to biological lineage; however, it is essential to expand the scope of family genetics for sensitive and impactful results in research with diverse communities. This need was recognized by genetic counselors at UBCH-CARD when interviewing individual family members to compile a pedigree. This biological information ultimately led to the discovery of EOFAD in this First Nation, but the complex social and cultural meaning of the family tree in the community required further exploration (Butler, Dwosh, et al., 2010).

Indigenous definitions of family and other social relationships are complex and unique from non-indigenous perspectives (Fuller-Thomson, 2005). Although there is great variation among First Nation communities, there are common values, understandings, and general guidelines for how to live within a community and family, including a strong sense of duty to family and the Nation, planning for younger generations, self-worth, consideration of surroundings, and commitment to equality (McCormick, 2009). In indigenous communities, family is particularly important to develop a sense of identity and connectedness in relation to culture. Family units serve as a source of value orientation, lifespan socialization, and cultural revitalization (Red Horse, 1997). It is the primary unit of kinship and culture, which fosters feelings of spiritual and cultural belonging (Walker & Shepherd, 2008). This kinship is often the major organizing principles of social life in indigenous communities, and households are often complex and large (Morphy, 2006). The complex nature of First Nations families can be reflected in unspoken adoptions within communities and families, skipped-generation parenting in which grandparents take primary care of their grandchildren (Fuller-Thomson, 2005), and a high proportion of extended family and community involvement in formal child and family welfare services (Blackstock & Trocme, 2005).

At the core of many indigenous worldviews is the interconnectedness of all creation (King, 1990). "All my relations" refers to the interdependency between individuals, family, community, Nation, and creation (McCormick, 2009). It reflects the fundamental view that all elements of life are related to one another. Consequently, indigenous conceptualizations of family may include not only socially and biologically related kin but also extend outward to encompass all human beings and elements of the environment. Indigenous peoples' conceptions of health also reflect interrelatedness as a balance of the physical, mental, emotional, social, and spiritual. An individual's wellness is supported by a strong, stable, and healthy community, which is dependent on family structure and functioning (Alfred, 2011).

First Nations concepts of extended family and holistic worldviews have implications for genetics research and clinical practice. Genetics research reaches beyond individuals to affect all familial relationships and brings the biological definition of family to the fore. Our research highlights three major issues for exploration about the relationship between traditional indigenous understandings of family and genetic diseases: (1) the tension between biological relationships and cultural beliefs about peoples' origins; (2) the social basis of caring within the community; and (3) the role of cultural status, particularly of First Nation Elders, in experiencing neurodegenerative disease and genetic research.

## Genetic Biomedical Explanations and Origin Stories

The basis of biological relationships in genetics can contradict cultural views and origin stories of family. In First Nation communities, as well as many other cultures, there are diverse forms and functions of families. By utilizing biological lineage as the primary variable of study, genetic research and clinical genetics imply that familial identity is derived solely from genetics (Campbell & Leckey, 2010). This can be at odds with cultural conceptualizations and experiences that have existed throughout many generations. TallBear (2007) highlights that "indigenous [peoples'] ways of understanding their origins [are] based in particular histories, cultures, and landscapes"; he continues, "The question of how we as [indigenous peoples] got to where we are has already been answered, and the answer is not one of genetics" (p. 416). Linear genealogy also poses the risk to highlight any inconsistency between traditional bloodlines and biological family, which could isolate some members of a cultural group (Pullman & Arbor, 2009).

Origin stories extend to health and wellness by providing cultural frameworks and explanations for certain diseases. For example, the familial risk of retinitis pigmentosa, an inherited form of blindness, is explained by a curse in the Tlicho Nation (Ponchillia, 2001). The story engendered feelings of shame within the biological family and disrupted the ability of family members to seek care. Western genetics offers another explanation of disease and has the potential to reduce this shame, although it may also increase isolation if it is taken to supersede cultural teachings. In another study, dementia has been described by the Secwepemc First Nation in British Columbia as a natural process of the life cycle in which memory loss has been regarded as returning to childhood (Hulko et al., 2010). The holistic view that memory loss is "an accepted part of the family cycle" (Hulko et al., 2010, p. 329) may imply infantizing older adults as they age, but in First Nations culture, children are highly valued as having close spirituality, suggesting that aging Elders with memory loss are returning to heightened spirituality (Hallowell, 2009). This conceptualization of dementia may be challenged by the neurogenetic model of EOFAD, and it signals the importance of critically analyzing the primacy of Western biomedical explanations in diverse cultural communities. The various ways that communities may pathologize illness highlight the significance of considering cultural beliefs in health. These beliefs have a significant impact on what individuals and communities may think is the cause of the illness, on the most appropriate ways to treat it, and about who they involve in medical care (Helman, 2007).

Decisions concerning genetic testing and evaluation of genetic risk are often grounded in social—not biological—relationships (Cox & McKellin, 1999). Social proximity to an affected person can be as important as biological relation when considering genetic testing for a hereditary disease (Gillet & McKergow, 2007). Diagnostic and predictive genetic testing for EOFAD typically requires pretest establishment of biological relatedness between the test-seeker and an affected family member with a confirmed EOFAD genetic mutation. In the case of our research with a First Nation community affected by EOFAD, both diagnostic and predictive genetic testing is available (and offered as a clinical service at UBCH-CARD) to *all* members of the Nation; individuals interested in pursuing the option of such testing are not required to demonstrate direct relationships with an affected family member (Mackie et al., 2012). Although this enables individuals to pursue genetic testing options without disrupting established definitions of family, pre-test genetic counselling would address the possibility that an individual's test results may reveal unexpected biological connections.

## Prominence of the Social Family as Caregivers

Along with providing a connection to kinship and culture, First Nation family units act as primary sources of caregiving and support. The Nation at the center of this study is required to provide most care within families because health services and support are limited in such remote and geographically dispersed populations. Care within the community is highly valued and guarantees culturally appropriate practices. This also stems from a strong intergenerational expectation that the community will take care of its own people through informal caregiving (Buchignani & Armstrong-Esther, 1999). It can be anticipated that an "Elder would continue to be supported and to support others while completing their journey through the full circle of life" (Hulko et al., 2010, p. 334). Traditionally, many generations and relations were involved in the care of Elders and other community members. This extended network of support is the cornerstone of caring in First Nations communities, and our research points to a sense of pride in the attentiveness of community members. This cultural and social structure of care highlights the importance of an expansive definition of family and the practical implications to providing support and care.

Genetics technologies, such as diagnostic and predictive tests for EOFAD, also pose a risk of medicalizing kinship and challenging the socioemotional ties that define family and structure caregiving (Cox & McKellin, 1999). This is an inherent risk when doing genetics research with any cultural group, but it may be particularly important to consider with a disease that requires such intensive care as EOFAD and with First Nations given the established significance of nonbiological relationships and the role of the family unit within the community.

### The Role of Elders in EOFAD Research and Caregiving

In indigenous communities, Elders are considered the guardians of culture and have the responsibility to "safeguard knowledge that constitutes the unique inheritance of the Nation" (Royal Commission on Aboriginal Peoples, 1996). Given this unique social position with families and communities, Elders could offer unique insight into how definitions of family and community relations may be impacted by inheritable diseases, diseases of aging populations such as AD, and genetic research. Given the larger context of "all my relations," it may be fruitful to facilitate decision-making around medical genetic research and clinical care that includes consultation with the extended biological and nonbiological family, including special consideration of Elders.

### Implications for Research: Cultural Considerations of Family in Genetic Research With Diverse Communities

The dominance of biological family in genetic research has the potential to contradict and, at worst, disrupt extended family relationships. Researchers and clinicians should be aware of the prominence of the social family in subjective risk assessment and care provision. It is essential to balance traditional cultural beliefs and practice with the requirement of using biological lineage in genetic research. Cultural competence should be the foundation of discovery in genetics, fueled by meaningful collaboration with the community being researched. Studying the experiences of a First Nation predisposed to EOFAD illustrates how the consideration of diverse cultural understandings will influence the process, results, and impact of the research.

### Incidental Findings, Culture, and Community Consent

As questions about culture interact with questions in medical research, the possibility of incidental findings and how to manage them arises. An incidental finding can be described as an "observation of potential clinical significance unexpectedly discovered in healthy subjects or in patients recruited to . . . research studies and unrelated to the purpose or variables of the study" (Illes et al., 2006). Most literature on incidental findings considers the ethical implications for an individual research participant and provides guidance on fostering a consent process that incorporates the potential for unanticipated findings (Illes et al., 2006; Wolf, Kahn, Lawrenz, & Nelson, 2008). The literature also describes the ethical and logistical complexity of delivering the information of the findings back to the individual research participant (Wolf et al., 2008).

Incidental findings in the context of an indigenous community are a topic we have explored in previous work (Brief, Mackie, & Illes, 2012). Alongside the work of Shuldiner, who has discussed the issue with respect to Amish populations (cited in Couzin-Frankel, 2011), we have provided guidance based on theoretical analysis of the issues. In this section, we briefly discuss the issues that emerge when an individual participates in research as a member of a socially identifiable population that has, as a community, consented to the research. Again, community-based research sets the parameters from which cultural neuroscience may engage with these ethical concerns in a manner that is of relevance to the community and of significance to the research.

Individual ownership of genes is based on Western ideas of individualized property. How, then, can researchers uphold the Western ethical standard of privacy of individual medical information and simultaneously honor cultural values and pragmatic considerations that may be in conflict with those standards (Gillett & McKergow, 2007)? Within an indigenous research context, when might community members and community agencies have rights to individual findings? We suggest that many ethical issues can be addressed by involving community members in guiding a research study and, in the context of incidental findings, in a pre-study, pre-launch stage of work (Brief et al., 2012). This requirement has become particularly acute as new clinical recommendations from the American College of Medical Genetics now urge that certain genetic findings unrelated to a primary inquiry must be returned to patients (Green et al., n.d.), a shift from the respect for autonomy that will surely have an impact on research practice.

## Researcher Responsibility to Individual and Community

In literature related to neuroimaging, Illes et al. (2006) have argued that research protocols should prepare for the possibility of incidental findings upfront and that transparent plans for managing them should be articulated both to review boards and, during the consent process, to prospective participants. These authors have shown that participants would prefer to be informed of anomalies detected in the brain, regardless of their significance or potential actionability (Kirschen, Jaworska, & Illes, 2006). To date, most discussions on the return of incidental findings are based on the idea that genetic, brain, and other physiologic and biologic data are personal property. Arguments for and against return of results adhere to Western ethical frameworks focused on individual rights (e.g., *Belmont Report*; Beauchamp and Childress, 2009). Discussion about the potential communal effect of the return of results of individual incidental genetic findings in socially identifiable populations is still largely absent from the discourse. Consequently, there are no guidelines about how a communal consent process could be designed with respect to incidental findings.

We have proposed that researchers must engage with communities to define, a priori, to whom incidental findings belong and to whom results should be returned and also the processes for fulfilling this commitment before the biomedical research is ever initiated (Brief et al., 2012). We further emphasize the importance of incorporating both individual and communal values to determine the threshold of clinical significance for the incidental findings to be returned and the need to preserve the privacy of individual health information. For example, Port, Arnold, Kerr, Gravish, and Winship (2008) describe how a Maori tribe modified the clinical genetic service provided to them to make the process of receiving results from genetic testing more culturally appropriate. Maori culture operates within a tribal hierarchy in which individual rights, including the right to privacy, may be relinquished to maintain tribal structure; the Maori culture emphasizes collectiveness, and even the ownership of genes and their mutations is shared by the entire extended family, or *whanau* (Port et al., 2008). Furthermore, Maori culture operates within a tribal hierarchy, in which individual rights, including the right to privacy, may be relinquished to maintain tribal structure (Port et al., 2008). In Maori and other indigenous populations, the Western emphasis on respect for personal autonomy and individual rights and risks may not adequately address the integral role that these communities play in ensuring their own protection in research settings.

The return of incidental findings has implications for individuals, their communities, and their health and social institutions. It is not reasonable or ethical to espouse a pan-indigenous solution for the 300–350 million indigenous people worldwide, representing 6% of the world's population and 5000 distinct peoples in 72 countries. However, a pan-research solution can be adopted to ensure that researchers fulfill their responsibility to understand specific perspectives of community in how to handle unexpected findings. A pan-research solution also cautions against assuming that Western ethics provide the answer, and it recommends development and implementation of a management plan for unexpected findings specific to community through a pre-research engagement process that is mutually informed and fluid to accommodate the dynamic nature of science.

## Conclusion

Our research and the considerations presented here suggest that culturally diverse communities experience the impact of neurodegenerative disease and neurogenetic research in unique ways. Culture mediates understanding and responses to change in brain health, and it shapes the way individuals respond to developments in neuroscience. There are distinctive explanations and descriptions of what is normal and abnormal in brain functioning, as well as value judgments about what requires intervention and what may not. Culture impacts how individuals and communities cope with cognitive decline and personality change, and it influences their experience from the first recognition of symptoms to long-term care.

It is essential that unique cultural experiences and perceptions are identified in parallel with the progress of innovation in neuroscience and taken into consideration when introducing new research and interventions. Qualitative, community-based research captures these unique experiences and has the transformative potential to involve and empower diverse communities. It has the potential to lead to better, more relevant research that will have a long-lasting, positive impact on the community. Our work provides further support for the recognition that culture largely shapes perceptions and experiences of brain health and disease and that neuroscience exists within, and not in isolation from, cultural processes.

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CHAPTER

12

# Quantifying Culture: The Cultural Distance Hypothesis of Melodic Expectancy

Steven M. Demorest *and* Steven J. Morrison

**Abstract**

All normally developing children acquire an understanding of the music and language of their culture without explicit instruction. This is known as enculturation. The process of musical enculturation is not well understood, but researchers have hypothesized that some form of statistical learning similar to that which influences language acquisition may underlie musical enculturation as well. We propose a "cultural distance hypothesis" that posits predictable expectation and memory responses for out-of-culture music based on a statistical comparison of that music with the listener's first music. The hypothesis is based on work in computer modeling of melodic expectancy as well as our own work in cross-cultural music understanding. We propose a series of studies to critically test the hypothesis and discuss implications for other domains of cultural neuroscience.

**Key Words:** cross-cultural, music, cultural distance hypothesis, cultural neuroscience, melodic expectancy

When considering culture as a construct by which humans organize themselves, few aspects of human behavior function as efficiently and effectively as music to characterize identity within and differences between cultural groups. Music is a universal phenomenon in that it exists in virtually every human society. At the same time, culture-specific music practices abound to the extent that a given music type can be reliably associated with a particular cultural group. Indeed, when referring to different music types (or "musics"), it is common practice—using terminology from the iTunes store as an example—to simply identify them by the society from which they emanate (e.g., Western European art song, Cajun music, and J-pop) or the cultural group with which they are most closely identified (e.g., Celtic folk music and Latin alternative), geographical boundaries notwithstanding. Music–cultural distinctions might also be identified across time (medieval plainchant, baroque sonatas, and big band jazz) and age (styles prevalent among children vs. "tweens" vs. twenty-somethings) as well as geography.

The ubiquity of music as a universal phenomenon tempts one to view it as a largely barrier-free means of expressive communication. Indeed, Longfellow's (1865) poetic notion that "music is the universal language of mankind" (p. 202) is readily referenced when observing the broad sweep of human music-making. One need look no further than the opening ceremony of the Olympic Games to witness attempts to use music as a vehicle to transcend national identities and bind an international population of participants, audience members, and viewers alike. Interestingly, these same ceremonies typically take the opportunity to highlight the unique characteristics of the host's music tradition, from the massed assembly of *Fou* drummers at the 2008 Beijing games to the music of the Beatles heard throughout the London ceremony in 2012. This juxtaposition of universality and cultural specificity highlights aspects of music that may be generalizable across cultural groups versus those particular to a specific group.

Evidence demonstrates that the boundaries between different music traditions are consequential to the way in which individuals process and interact with "their" music and that of "others." Cognitive processes such as memory appear to function more efficiently and more effectively in the presence of music that is based on a familiar set of rules and conventions even when a specific music example is entirely novel to a listener. In contrast, music that is derived from a culturally different set of organizational principles can prove difficult for a listener to organize, encode, and recall. The question, then, is, "What makes culturally unfamiliar music so unfamiliar?"

The purpose of this chapter is to propose a specific hypothesis that can facilitate an understanding of the process by which culture-dependent music knowledge is acquired. We believe that cultural familiarity is a product of the degree to which relationships within musical structures—specifically those relating to pitch organization—conform to one's implicitly learned expectations, schemata through which individuals define, interpret, and evaluate musical information. Furthermore, we believe that a consequence of this proposition is the necessity of viewing cross-cultural music interactions[1] as taking place along a continuum of facility, a "cultural distance" that may predict specific cognitive outcomes. We propose that the extent to which melodic pitch relationships in examples of culturally unfamiliar music correspond to those of one's own cultural practice can predict culturally dependent responses such as preference, tension, expectation, and memory. By suggesting that the effectiveness with which one can perceive, encode, and retrieve culturally unfamiliar music is related to its statistical properties, we offer a model that may be useful in connecting cross-cultural research in music cognition to other areas such as own-race effects in facial recognition (Lucas, Chiao, & Paller, 2011) or fundamental aspects of language acquisition (Kuhl et al., 2008).

## Universality and Specificity

The popular view that music is universally understood[2] may stem in large part from the seemingly imprecise nature of its content. In contrast to language[3], music—absent text or other linguistic content—does not communicate specific propositions. A musical work can function more like a canvas onto which listeners can project their unique interpretation. Although there are certain musical gestures that can be emblematic of a specific idea, image, or entity (e.g., the "Call to Post" is a common musical reference in the United States to the start of a horse race), the music itself does not convey this information, only its well-established association with the thing being referenced. It has been proposed that it is this very imprecision of "meaning" that allows music to function so effectively as a social binding agent, a characteristic Cross (2008) refers to as "floating intentionality" (p. 157). Each individual may have a slightly different experience with a given musical event, but that difference lies within a range of possibilities that does not disrupt social cohesion. In fact, there is evidence that music may be vital in promoting human interaction in terms of prosocial behavior (Rabinowitch, Cross, & Burnard, 2013), movement coordination (Kirschner & Tomasello, 2009), and physiological synchrony (Vickhoff et al., 2013).

Besides a *sense* of shared-ness across musical experiences, all humans share the machinery and neurological substrates by which musical information is perceived. The manner in which sound is detected and processed relies on biology common across the width and breadth of the species. Unlike hearing physiology that is readily observed and easily tested, the neural systems employed in the processing of music have been examined and charted among a relatively smaller and less representative sample of the world's population. Nevertheless, the neural architecture in which music is processed appears remarkably similar across cultural groups, although exceptions have been reported, such as between groups who do or do not speak tonal languages

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[1] For extensive reviews of cross-cultural research in music cognition, see Morrison and Demorest (2009), Stevens (2012), and Patel and Demorest (2013).

[2] Both Nettl (2000) and Brown and Jordania (2011) offer thorough examinations of universals in music.

[3] In the study of music as a cognitive process, it is often helpful to look to language as a conceptual or structural analog. In some instances, evidence has been found suggesting shared processes for both phenomena (e.g., Patel, 2008; Saffran, Johnson, Aslin, & Newport, 1999; Steinbeis & Koelsch, 2007). Likewise, there is significant methodological overlap in research designs used to investigate both music and language. However, it is erroneous to simply equate music with language—even cautiously—despite the common view of music as a "universal language." The complex relationship between music and language is far beyond the scope of this chapter. Where appropriate, we clarify when references to language are intended as a general comparison and when they describe actual overlapping, shared, or unique processes.

(Wong et al., 2012). Few studies have employed neurological measures to directly compare music processing across cultures. However, listeners from varied cultural groups demonstrate generally consistent increases in right lateralized activity to violations of expected musical events (Demorest & Osterhout, 2012; Nan, Knösche, & Friederici, 2006). Similar responses have been observed among within-culture listeners trained in different music traditions (Tervaniemi, Tupala, & Brattico, 2012). Functional magnetic resonance imaging (fMRI) data indicated greater activation in right frontal areas among listeners encountering unfamiliar phrase structures (Nan, Knösche, Zysset, & Friederici, 2008), unfamiliar chord progressions (Koelsch, Gunter, Friederici, & Schröger, 2000), and encoding and retrieval of out-of-culture music (Demorest et al., 2010).

In addition to the mechanics of hearing and the fundamental systems of music processing, commonality has also been observed to a limited extent in the area of affective response. Although it would be inaccurate to characterize music's emotional content as universal, basic broad categories of emotion (e.g., happiness, sadness, and anger) appear to be discernable in culturally unfamiliar music performances to listeners from a range of cultural backgrounds (Fritz et al., 2009; Laukka, Eerola, Thingujam, Yamasaki, & Beller, 2013). It has been proposed that the affective content of music arises from a combination of acoustic characteristics that can mimic the physical qualities of emotional states (e.g., sad and slow, happy and bright) and embedded cultural cues (Balkwill & Thompson, 1999). Whereas the former are interpretable to listeners from both within and outside a cultural group, culture-specific cues are only accessible to in-group members.

Two other factors that contribute to the seeming universality of music are the pervasiveness of a few particular music traditions throughout so much of the world and the easy accessibility to so many different music types. Despite its identification with Western European culture of the eighteenth and nineteenth centuries, "classical" music is commonly encountered and studied throughout the world (e.g., see Kahn & Wakin, 2007). Furthermore, its system of diatonic harmony and associated hierarchical pitch structures (with tones having distinctive relationships to a specified pitch center or "key") forms the basis of many popular music styles, including rock, pop, country, and jazz, each encountered and consumed the world over. In addition to the ubiquity of styles based on Western tonal principles, innumerable types of music are now instantly accessible via digital media. Platforms such as YouTube, streaming music services such as Pandora, and remote access to radio stations from throughout the world offer opportunities to encounter an endless array of unfamiliar musics and to synthesize these styles and practices into yet newer forms and genres. The reach of on-demand global media can render musical boundaries more permeable while at the same time reminding us how many musical boundaries there are.

Despite such a broadly universal view of human music-making, the realities of global musical practice reveal the seemingly infinite variability that exists between music traditions. There are many ways to examine culture-specific aspects of music. For our present purposes, it may be helpful to define musical enculturation as a process that addresses both how music is *used* in a culture (how individuals learn music's *function*) and how it is *constructed* by the culture (how individuals implicitly learn salient *characteristics* of music), with the latter more germane to the topic we address here.

The use of music in any given cultural context can include activities ranging from the large scale and communal to the individual and personal (Boer et al., 2012). Rituals such as religious ceremonies, festive celebrations, and courtship practices often include substantial and, in some cases, very specific musical content. On a more private level, music also often accompanies activities such as meditation or the pursuit of solitary livelihoods. Recent attention has been given to the importance of music in personal health and individuals' maintenance of a sense of well-being (Ruud, 2013). Qualitative evidence describes the use of music both as an ameliorative agent and as a means of emotional and physiological self-regulation (Creech, Hallam, Varvarigou, McQueen, & Gaunt, 2013; MacDonald, 2013).

Regardless of the scale of the musical interaction, music can serve as a focal point for culture-specific behavior and a backdrop for cultural identity (Frith, 1996). However, it is not always necessary that differences in identity demand differences in music structures. The school song of State U may be a rallying point for its students and alums, but it is not different in structural substance from the song of a much-despised rival from a neighboring state. Likewise, differences between West Coast and East Coast hip-hop—each of which boasts its own set of artists and fans—are rooted more in subtly divergent stylistic approaches than in fundamentally different formal principles (a contrast paralleled by West Coast and East Coast jazz styles from a half century earlier).

Nevertheless, the ubiquity of culture-based music styles (or genres, types, traditions, or practices—the terminology can be tellingly imprecise) suggests some degree of difference in formal substance among the world's varied traditions. Simply stated, musics of different traditions *sound* different. Moreover, these differences require culture-specific knowledge for a listener to gain access to the formal principles at play. Such culture-specific knowledge leads to differences observed between individuals from different cultural groups on such music-based tasks as preference evaluation and written description (Morrison & Yeh, 1999), phrase parsing (Nan et al., 2008), memory (Demorest, Morrison, Jungbluth, & Beken, 2008), rhythmic synchronization (Drake & El Heni, 2003), and metric organization (Hannon & Trehub, 2005a, 2005b). To examine the nature of these and other culture-based differences, it is essential to consider the process by which one develops knowledge of his or her own musical culture.

## Musical Enculturation

In order for one to function as a member of a musical culture, at some point in time he or she must undergo a process of enculturation. The process by which we learn "our own" musical system is informal insomuch as it is not acquired through a course of prescribed lessons, a particular instructional sequence, or a music textbook series. It is learned through repeated interactions with the prevailing musical culture in the form of play songs, lullabies, commercial jingles, television and movie soundtracks, radio programming, Internet videos, and myriad other sources. Although informal, this process is powerful, ultimately resulting in a level of perceptual skill and knowledge that can be indistinguishable from that typically associated with extended formal training (Bigand & Poulin-Charronnat, 2006). Except in cases of severe cognitive deficits (e.g., congenital amusia (Ayotte, Peretz, & Hyde, 2002)), individuals acquire a thorough knowledge of the formal and organizational principles characteristic of the musical practice common in their environment.

The manner in which music is organized varies from culture to culture. Aspects of musical structure such as pitch, rhythm, meter, and form follow norms established by tradition and practice, sometimes dating back centuries. In some cases, accepted practices have been codified into formal theoretical terms such as with the classical traditions of India or the "common practice period" of European music. In other cases, knowledge of accepted norms is shared less formally (although not necessarily less rigorously) among practitioners, such as with conjunto music of the Texas–Mexico border region or the Amhara songs of northern Ethiopia.

Regardless of the formality with which its rules and conventions are delineated, music knowledge is acquired much like any other cultural practice through a mix of observation (which, in the case of music, includes listening) and active engagement that persists throughout childhood (Campbell, 2010; Henrich, 2008). Children's acquisition of culture-specific music knowledge appears to be a bottom-up process beginning with infants' abilities to distinguish between categories of musical information (e.g., consonant and dissonant intervals (Trainor, Tsang, & Cheung, 2002)) and between contrasting musical patterns (such as with disrupted metric patterns (Trehub & Hannon, 2006)). Sensitivity to characteristics of one's own musical culture appears increasingly evident at approximately 12 months of age, at which time children have been observed to lose sensitivity to violations in out-of-culture rhythm patterns (Hannon & Trehub, 2005b) and scales (Lynch & Eilers, 1992), which corresponds to the point at which infants also begin to lose sensitivity to non-native linguistic information (Kuhl, 2004).

Past infancy, the ability to quickly acquire knowledge of culturally unfamiliar music appears to become much more difficult. One might speculate that there is a significant challenge in learning a new musical system while already possessing knowledge of a "first" music. A predilection to simply accommodate new musical information using old cognitive strategies may mitigate against the establishment of new, culturally specific schemas and rule systems. Indeed, both adolescents and college students have demonstrated poorer memory for out-of-culture music even after extended study of that music (Demorest et al., 2008; Morrison, Demorest, Campbell, Bartolome, & Roberts, 2012). In contrast, no such difference was observed among adults who had been encultured to two different music traditions from birth (Wong, Roy, & Margulis, 2009). Such findings, discussed in detail next, highlight the difficulties of crossing music–cultural boundaries and reveal some of the cognitive implications of one's position as a cultural "insider" or "outsider" (Rice, 2008).

## The Enculturation Effect in Music Cognition

A number of studies have explored the influence of enculturation on music processing by using memory performance as a proxy for musical understanding (Demorest et al., 2008, 2010; Morrison, Demorest, Aylward, Cramer, & Maravilla, 2003; Morrison, Demorest, & Stambaugh 2008; Wong et al., 2009). The premise of these studies was that if culture influenced music cognition, then culturally unfamiliar music would be more difficult to process and remember. For example, Demorest et al. (2008) asked musically expert and novice listeners from the United States and Turkey to listen to short instrumental excerpts from Western art music, Turkish art music, and Chinese traditional music. All of the excerpts were unfamiliar to the listeners and were matched as much as possible for tempo, texture, and instrument families. After hearing a block of examples from each culture, the listeners took a memory recognition test with old and new items and were asked to identify which had been heard before. Both the US and Turkish subjects were significantly better at remembering novel music from their home culture than either of the other cultures presented, although Turkish listeners did show a difference between Western music, to which they had had some exposure, and Chinese music, to which they had had little or no exposure. As in other music memory studies (Halpern & Mullenseifen, 2008; Korenman & Peynircioglu, 2004; McAuley, Stevens, & Humphreys, 2004), there was no difference in memory performance due to formal music training. It appeared that culture was the crucial variable in listeners' ability to encode and retrieve musical information of different styles.

These same results have been found when the subjects were children instead of adults (Morrison et al., 2008, 2012) and when the musical material was simplified (Morrison et al., 2008; Wong et al., 2009). Wong et al. tested listeners from the United States and India and found that memory performance clearly distinguished between mono- and bicultural individuals. Demorest et al. (2010) used the same testing procedure as the 2008 study with subjects from the United States and Turkey except that it was performed while subjects underwent an fMRI scan. They found that although subjects performed best on the culturally familiar music and showed similar patterns of activation for both the encoding and the memory phases of the study, they experienced significantly *greater* brain activity when processing the out of culture music, particularly in right frontal areas, right angular gyrus, and posterior precuneus. A similar increase in activation has been found in other comparative musical tasks (Nan et al., 2008) and has been interpreted in other domains as reflecting a greater cognitive load in the encoding process (Baker, Sanders, Maccotta, & Buckner, 2001; Buckner & Wheeler, 2001; Holcomb et al., 1998).

Although the results of these studies paint a consistent picture of the influence of culture across different kinds of music and under different listening conditions, they do not reveal what feature or features of the musical material might trigger a culturally biased response. For example, simpler musical material yielded a better overall memory performance than complex material (Morrison et al., 2008), but the within-subject difference in memory performance by culture actually increased slightly, suggesting that simplification may have enhanced cultural differences rather than reduced them. In a recent study (Demorest, Morrison, Bodnar, & Nguyen, 2015), we attempted to isolate specific musical features that might trigger an encultured memory response. To do this, we used the same procedures outlined previously but randomly assigned listeners to one of three conditions of decreasing contextual information: (1) the original full ensemble recordings, (2) melodies alone transcribed and played back in piano timbre without expression, and (3) isochronous (equal rhythm) melodic pitch sequences in piano timbre. Whereas changing the musical context did influence memory performance significantly for in-culture music, it had no influence on memory performance for out-of-culture music. Overall, out-of-culture music memory was significantly worse than in-culture performance in all three contextual conditions, and the *d*-prime scores for out-of-culture memory tasks, although better than chance, were statistically identical regardless of context. Thus, for an out-of-culture listener, music memory was the same whether one heard a full ensemble performance, the melody alone, or just the isochronous pitch sequence of a song. This suggests that encultured responses to music are at least in part the result of expectancies generated solely by the note-to-note relationships between pitches. If enculturation influences melodic processing at the level of pitch sequences, then it suggests that part of becoming an encultured listener is the implicit learning of the commonly occurring sequences of pitches within the culture.

## Enculturation and Melodic Expectancy

All normally developing children acquire an understanding of the music and language of their culture without explicit instruction. As mentioned previously, cultural differences in responses to music and language emerge by at least 12 months of age (Hannon & Trehub, 2005a, 2005b; Lynch & Eilers, 1992; Schellenberg & Trehub, 1999; Werker & Tees, 1984). Some scholars have hypothesized that implicit acquisition of language is guided by a fundamental process known as "statistical learning" (Kuhl, 2004; McMullen & Saffran, 2004; Saffran, Aslin, & Newport, 1996). The premise of statistical learning is that infants subconsciously track information about the distributional frequency with which certain items occur and the likelihood (transitional probability) that one sound unit will follow another in a given language. This enables them to perceive larger patterns in continuous auditory stimuli such as language and music, often with relatively brief exposure, based on how often the smaller units of those patterns (i.e., phonemes or notes) occur together. This frequency of co-occurrence is known as the "transitional probability" of two or more sounds.

In a series of experiments, Saffran and colleagues manipulated the transitional probabilities of a series of nonsense syllables (Saffran et al., 1996) and musical tones (Saffran, Johnson, Aslin, & Newport, 1999). After exposure to streams of information containing linguistic or musical "words," adults and 8-month-old infants were able to distinguish the patterns that had occurred together with the highest frequency from those that had not. Furthermore, the extent to which the patterns in both domains were learned corresponded to the differences in their transitional probabilities. The authors concluded that "the same statistical learning mechanism can operate on both linguistic and nonlinguistic stimuli. Thus at least part of the machinery involved in natural language learning may be shared with other pattern learning processes" (Saffran et al., 1999, p. 47).

One consequence of the statistical learning process is gradual insensitivity to stimuli that do not conform to more frequently occurring patterns of native speech. At the neurological level, such learning results in what Kuhl (2004) described as native language neural commitment (NLNC):

> According to NLNC, language learning produces dedicated neural networks that code the patterns of native-language speech. The hypothesis focuses on the aspects of language learned early—the statistical and prosodic regularities in language input that lead to phonetic and word learning—and how they influence the brain's future ability to learn language. According to the theory, neural commitment to the statistical and prosodic regularities of one's native language promotes the future use of these learned patterns in higher-order native-language computations. At the same time, NLNC interferes with the processing of foreign-language patterns that do not conform to those already learned. (p. 838)

If musical understandings are acquired through a statistical learning process similar to language, then something like NLNC may occur with musical enculturation. Because culturally biased responses to both music and language begin to emerge at the same age, it is likely that the musical patterns of one's native culture result in a neural commitment that interferes with future learning of a different system. If so, then in order to better define and test the process of musical enculturation, it would be important to know which statistical properties of music show the greatest variability between cultures and therefore may be driving N*M*NC or a native *music* neural commitment process.

Pearce and Wiggins (2006) tested a statistical learning algorithm for Western music as a computer model to mimic human expectancy judgments. The computer model's performance was compared to human judgments from previous expectancy studies (Narmour, 1990; Schellenberg, 1997). Their results suggest that statistical learning plays a role in developing our implicit knowledge of music and our expectations for music of our culture. Although some studies have suggested that the transitional probabilities of artificial musical structures can be acquired quickly in laboratory situations (Loui, Wessel, & Kam, 2010; Saffran et al., 1999), given the timeline over which the NLNC or NMNC process appears to occur, this likely does not apply to the kind of permanent learning gained in more naturalistic environments. For example, Morrison et al. (2012) found that immersive instruction in culturally unfamiliar music did not significantly improve memory performance among elementary students relative to music of their own culture. In previous writings (Demorest & Morrison, 2003; Morrison & Demorest, 2009), we have hypothesized that listeners in an out-of-culture memory task may attempt to use their Western-encultured schematic understanding of music to interpret out-of-culture musical examples rather than developing a new, more culturally appropriate schemata. This hypothesized accommodation is consistent with a neural commitment theory description of learning in which the development of a new cultural schema is prohibited. Such an accommodation leads to an impoverished memory for music from unfamiliar cultures, especially in cases in which that music is organized according to very different structural principles.

## The Cultural Distance Hypothesis

If our understandings of out-of-culture music are filtered through in-culture expectations, then a comparison of the statistical properties of a listener's home music with that of an unfamiliar music culture will yield predictive information about subsequent memory performance. That is, the more statistically different two musics are, the worse a listener from one culture would do in music processing tasks such as memory or deviation detection in the other culture. This difference could be thought of as the "distance" between two cultures' musically. We propose a "cultural distance hypothesis" of music enculturation, which states that

> the degree to which the musics of any two cultures differ in the statistical patterns of pitch and rhythm will predict how well a person from one of the cultures can process the music of the other.

If such a distance can be quantified according to a particular inductive set of melodic statistics, it may yield insights into the implicit learning process of enculturation. The question then becomes, How would one go about determining the statistical properties of musics from a variety of cultures?

One of the most influential theories of Western music cognition has been expectancy theory (Huron, 2006; Meyer, 1956). Expectancy theory posits that music listening is a process of prediction, that the enjoyment and meaning we derive from musical utterances comes from the way a particular piece of music manipulates our learned expectations of what should come next. According to this theory, emotional responses to music are a result of expectations being violated, delayed, or resolved. Researchers and theorists have generated rule-based models to explain how the process of music expectancy functions at the level of human judgments about melody (Narmour, 1990; Schellenberg, 1997). These models generally combine both top-down (based on prior knowledge) and bottom-up (based on the patterns of the stimuli) rules in some combination to try to predict how humans will hear and respond to music.

More recently, researchers have developed computational probabilistic models of expectancy formation (Pearce, 2005; Pearce, Herrojo Ruiz, Kapasi, Wiggins, & Bhattacharya, 2010; Pearce & Wiggins, 2006, 2012) that take advantage of modern computers' ability to sift and analyze large bodies of data. The programs analyze the statistical properties of pitch, rhythm, and harmony patterns from a large body or *corpus* of music and generate an inductive, probabilistic set of rules that model a particular style of music. Researchers then expose this model to new input from the same tradition that was not included as part of the original corpus and compare the response of the model to that of human beings. Pearce and Wiggins (2006) used a program called IDyOM, which employed a statistical learning algorithm, to analyze a large corpus of Western music consisting of 152 Canadian folk songs and ballads (Creighton, 1966), 185 of the chorale melodies harmonized by J. S. Bach (Riemenschneider, 1941), and 566 German folk songs from the Essen Folk Song Collection (Schaffrath, 1995). Once the model was "trained" using these stimuli, it was exposed to new stimuli in three experiments representing three different melodic contexts: single interval continuations, British folk melodies, and chorale melodies. In each case, the probabilistic model outperformed the best rule-based model (Schellenberg, 1997) in predicting human expectancy judgments. Although the model incorporated a number of musical variables in its analysis, relatively few of those variables were actually needed to predict human judgments. One of the most significant factors for all three experiments was "regularities in pitch structure defined in relation to the first note in a melody" (Pearce & Wiggins, 2006, p. 401). This variable matches well with the findings of our cross-cultural experiment on contextual influences in memory (Demorest et al., 2015), in which the pitch sequence alone generated a culturally biased memory response, suggesting that pitch structure may account for much of the in-culture bias in memory performance.

Although computational modeling studies have been limited to Western music thus far, it should be possible to analyze a corpus of melodies from two distinct musical cultures and compare their statistical properties on a variety of features, such as contour, interval, motive, or density. Predictions generated by these computer models could be validated by comparing them to the responses of listeners from several cultures in terms of hit/false alarm rates (Demorest et al., 2008, 2013; Morrison et al., 2008), strength of brain activation in memory tasks (Demorest et al., 2010), and magnitude of behavioral or event-related potential (ERP) responses to melodic deviations (Bischoff Renninger, Wilson, & Donchin, 2006; Demorest & Osterhout, 2012). Using the methodology from corpus studies such as those of Pearce and Wiggins (2006), we could test the validity of the cultural distance hypothesis through a series of studies.

### Testing the Hypothesis

The first step would be to identify a corpus of melodies from the Western tradition and another from a more theoretically distant music culture such as that of Turkey. An inductive computational modeling program such as IDyOM (Pearce, 2005) would then analyze the statistical properties of each corpus of melodies in MIDI format to generate “rules” for each.[4] By comparing the models generated by encounters with the two different corpora, we can get a sense of where and how the two musics differ in their structural melodic patterning. Once the computer models have been trained, they can be fed the stimuli that were used for previous studies of human performance. Provided that the corpus used for training the model is valid, the model response to new stimuli should mimic that of an encultured listener on both in-culture and out-of-culture music. By comparing the models generated by these analyses to data sets from previous studies of human cross-cultural memory performance, we can begin to understand which features from the corpus best predict human performance.

If we can identify a set of structural melodic variables that are significantly related to processing out-of-culture music, then a second test of the hypothesis would be to choose a subset of melodies from the corpus that either maximizes or minimizes the distance between the two cultures based on those features. These melodies could be used as stimuli in a new memory experiment. By using actual melodies from two different cultures, but manipulating memory performance based on the specific properties of those melodies, we can begin to isolate those musical features that account for culturally biased responses to music. A better understanding of those features has significant implications for music teaching. For example, teachers may choose to introduce children to other music cultures by choosing a repertoire that initially minimizes cultural distance. Once we understand which features seem to be driving encultured responses to music, we can begin to study the process of enculturation more systematically. This could lead to better approaches to cross-cultural music training perhaps with the goal of achieving bimusicality.

In addition to using these models to predict behavior, we can use the same models to predict neurological responses to out-of-culture music. Pearce et al. (2010) used an IDyOM analysis to predict expectancy responses to Western music in an ERP paradigm. A third test of the hypothesis would be to replicate that experiment but using stimuli from the cross-cultural corpora under study. By creating melodic deviations that violate both the tuning and the scale structure of one or both of the cultures under study, we can explore how well the cultural distance hypothesis would predict ERP responses to out-of-culture deviations. In previous ERP studies (Bischoff Renninger, Wilson, & Donchin, 2006; Demorest & Osterhout, 2012), listeners were less sensitive to deviations in out-of-culture music as evidenced by smaller incongruity ratings and by a reduced P300 or P600 magnitude. Studies with adults and among second language speakers have demonstrated a similar insensitivity to deviations in non-native speech that can change rapidly with intensive instruction (McLaughlin, Osterhout, & Kim, 2004). A longitudinal study with infants found that ERP sensitivity to non-native features of language begins to diminish between 7 and 11 months of age (Rivera-Gaxiola, Silva-Pereyra, & Kuhl, 2005). The cultural distance hypothesis would predict that the statistical distance between the two musics should be inversely correlated with the speed and magnitude of the P600 response to deviations in music of the unfamiliar culture.

A similar approach could be used to predict fMRI responses to out-of-culture music. Previous fMRI studies of cross-cultural memory (Demorest et al., 2010) or phrase identification (Nan et al., 2008) tasks have found significantly *greater* activation for processing out-of-culture versus in-culture music—a difference that has been linked to cognitive load demanded of unfamiliar music rule systems. The cultural distance hypothesis would predict

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[4] One unresolved question is whether the analyses of the two cultures would use the same set of features as a basis for comparison or whether Western concepts such as harmony or key might be replaced with more culture-free features such as note density or frequency of occurrence when analyzing a non-Western corpus of melodies.

that the statistical distance between the two musics would correlate with the blood flow responses such that greater distance yields greater differences in blood flow during a particular music cognition task.

## Conclusion

There are many potential benefits to developing a predictive model of cross-cultural music cognition. In addition to informing our ideas about the process of musical enculturation, the model can help to refine our current theories of melodic expectancy (Huron, 2006; Narmour, 1990; Schellenberg, 1997), which are based exclusively in music of the Western European tradition. A culturally broader theory of music expectancy has the potential to improve the cognitive neuroscience of music by supplying a more inclusive model of the fundamental processes of implicit learning in music. Such a model could provide a better framework for exploring neurological development in music and for understanding the role of music in cognitive development in general.

A second potential benefit is the application of the cultural distance hypothesis to other domains of cultural neuroscience. The hypothesis applies the processes of statistical learning and expectancy formation to the problem of musical enculturation and its impact on cognition. Because these processes are not musical per se, but are fundamental properties of human cognition, then it is reasonable to assume that the hypothesis could be applied in other cognitive domains in which feature detection and pattern learning are important. At the first meeting of the International Cultural Neuroscience Symposium, the question was raised, “Couldn’t this hypothesis be applied to other areas of cultural neuroscience?” For example, it has been suggested that the “other-race effect” or “own-race bias” in memory for faces is a result of familiarity with certain patterns of features and lack of familiarity with others (Lucas, Chiao, & Paller, 2011). The cultural distance hypothesis could provide a framework for exploring what quantity and type of facial features might account for cultural differences in face memory performance. It could also perhaps be used to predict which ethnic groups would have more difficulty recognizing and remembering facial features. Such information could be valuable in practical situations such as assessing the validity of witness testimony cross-culturally (Brigham & Ready, 2005; Meissner & Brigham, 2001). If responses to music can be predicted from an analysis of the statistical properties of music from a variety of cultures, it provides further evidence of the apparent overlap in music and language learning systems. It may be that the cultural distance hypothesis is a musical analog to Kuhl’s native language magnet theory of phonetic learning (Kuhl, Williams, Lacerda, Stevens, & Lindblom, 1992; Kuhl et al., 2008).

From the perspective of our field of music education and the related field of music therapy, the cultural distance hypothesis may offer teachers and therapists some guidance regarding their choice of materials. As therapists work in an increasingly multicultural society, they may find themselves at a loss working with patients whose musical traditions are very different from their own. A basic tenet of music therapy is that the patient’s musical preferences should be a starting point for intervention, but it is not clear how a therapist’s lack of cultural familiarity with certain material might affect therapeutic outcomes. Preliminary research examining different types of Western musicians (classical, jazz, and pop) suggests that culture can be an important variable in determining a therapist’s approach (Gonzalez, 2011).

In music education, many current approaches to multicultural music teaching delineate or imply a clear distinction between the familiar and the unfamiliar, a view that incorporates world music instruction as an opportunity to explore musical spaces well away from the known (at least that which can be considered known within the local musical mainstream). Alternatively, the construct of cultural distance frames music traditions as points on a continuum that originate at a point of greatest musical familiarity and move progressively outward (an observation that Fung (1996) has made in relation to music preference). Music traditions that share considerable characteristics with that which is familiar—those that can easily be accommodated by existing listening schemata—would be plotted quite close to this point of origin. In this model, the line between the familiar and the unfamiliar becomes blurred unless musical “loci” are selected with the intent of maximizing the distinction between them. If teachers are aware of which of the world’s musics share features with the local or dominant culture’s music, they can use that information to design learning opportunities that build on and expand students’ encultured understandings. Such information may be important for individualizing the instruction of children who have recently arrived from a different culture and do not yet share the encultured musical understanding of the rest of the class. Such information could also be used to guide the development of bimusical curricula so that musicians could become "fluent" in a second or third music. Future research may help us to understand what can and cannot be learned cross-culturally at different points in our development.

The world of music, especially popular music, does not view cultural boundaries as static entities that are difficult to cross but, rather, as sources of innovation to be borrowed and shared. Contemporary musicians freely draw from sources that are culturally, historically, and stylistically distant. Because of this attitude, we are currently experiencing a fusion (some might say homogenization) of the world's music into new hybrid forms—a collapse of diverse traditions, times, and identities into distinctive musical expressions. One could argue that many of these hybrid forms have their foundation in a Western popular music aesthetic. Consequently, those aspects of an indigenous music that do not fit the cognitive framework of that aesthetic either rhythmically or melodically may be "lost in translation" and begin to disappear from the culture. The process by which the great diversity of the world's musical expression that has sprung from the common well of our shared biology is one of the more compelling questions of neurological development. It may be a matter of some urgency to study those cultural differences while they still exist to provide a window into the enormous flexibility of human cognitive development.

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# PART 4

# Cultural Neuroscience of Social Cognition

## CHAPTER 13

# Cultural Neuroscience Studies of the Self-Reflection

Shihui Han *and* Yina Ma

**Abstract**

Self-reflection characterizes human thoughts. How the brain reflects on the self and relevant emotional consequences, however, varies significantly across individuals. This chapter discusses whether and how sociocultural/sensory experiences and biological factors, such as genes, influence the neural correlates of reflection on the self and close others. By presenting the findings of transcultural and cultural priming neuroimaging studies and the findings of imaging genetics, we suggest that both sensory and sociocultural experiences shape the pattern of neural activity involved in the cognitive processes during self-reflection. Genetic makeup, however, produces novel effects on the neural activity underlying the emotional consequences of self-reflection. The findings provide a cultural neuroscience framework for understanding of self-reflection and its relationship with mental health.

**Key Words:** self-reflection, functional MRI, culture, gene, sensory experience, *5-HTTLPR*

## The Self in Different Cultures

What is the self? This question has been the object of human contemplation for a long time. Ancient philosophers in the Western cultures took the existence of the self for granted. Aristotle (384–322 BC) argued that "the whole self, soul and body alike, is something given and not questioned." Aristotle also claimed that "knowing yourself is the beginning of all wisdom." Ancient philosophers in East Asian cultures also believed in the existence of the self. For example, a Chinese philosopher named Zengzi (曾子) (505–435 BC) asked his students to "reflect on the self many times a day." Even Buddhists who held the doctrine of "no-self" spend much time teaching why the idea of self is an imaginary false belief with no corresponding reality. Thus, people in ancient times must have realized the significance (either positive or negative) of self-concept and self-reflection for their lives.

However, the meaning of the self can be drastically discrepant across different cultures. In his book titled "The Idea of the Self," Seigel (2005) opened with the statement that "by 'self' we commonly mean the particular being any person is, whatever it is about each of us that distinguishes you or me from others." (p. 3) This proposition represents the Western thought of self-concept and has had a major influence on subsequent studies of the self in multiple disciplines. In contrast, the self is understood in a different manner in East Asian cultures. Rather than asking his students to consider what aspects of the self are different from those of others, Zengzi instructed his students to reflect on their faithfulness to their peers and their reputation among friends. Modern Chinese philosopher Shi-Ying Zhang argued that the whole universe, including nature, human society, and the spiritual domain, exists as a net of universal connection on which every thing is but a knot or a cross point: "A person is a knot in the net, with the only exception that he is able to consciously think of the self, i.e., has self-consciousness and is capable of transcending itself" (Zhang, 2005, p. 83). This proposition echoes an early statement by another Chinese philosopher, Shih Hu (1929/2006), that "a person can not exist alone; all action must be in the form of interaction between person and person" (p. 107).

There is now ample evidence that cultural traditions regarding how to think about the self produce significant effects on psychological processes related to the self and others. For example, human adults usually respond faster to images of their own faces compared to images of familiar or unfamiliar faces during judgments that require explicit (Keenan et al., 1999) or implicit (Ma & Han, 2010; Sui, Zhu, & Han, 2006) face-owner identification. However, the self-face advantage shown in behavioral performances is much more salient in British than in Chinese participants (Sui, Liu, & Han, 2009). Moreover, self-face recognition is more susceptible to the influence of viewing significant others in Chinese than in American graduate students; the presence of one's advisor's face significantly slowed responses to one's own face in Chinese but not in American students (Ma & Han, 2009; Liew, Ma, Han, & Aziz-Zadeh, 2011). These findings suggest that self-referential processing in the perceptual domain is shaped to a certain degree by individuals' cultural experiences.

Behavioral performances in a self-referential memory task (Rogers, Kuiper, & Kirker, 1977) show similar effects of cultural experiences. This memory task requires participants to make judgments on whether a list of trait adjectives can describe the self or a well-known public figure (e.g., a celebrity). Participants are then asked to recognize the words used during the judgment task. It has been shown that self-descriptive trait adjectives are better remembered than other-descriptive trait adjectives, and this finding defines a self-reference effect (Klein, Loftus, & Burton, 1989). Interestingly, it has been demonstrated that Westerners show a self-reference effect over close others such as mother and best friend (Heatherton et al., 2006; Klein et al., 1989). This indicates dissociation between the self and close others in memory in Western cultures. In contrast, Chinese participants remembered equally well trait adjectives that are associated with the self and close others (mother/father/best friend) during trait judgment tasks (Qi & Zhu, 2002; Zhu & Zhang, 2002), suggesting similar encoding and/or retrieval of information about oneself and close others in Chinese culture.

Both philosophical thoughts and empirical findings suggest differences in self-concept as perceived and defined by Western and East Asian cultures. According to Markus and Kitayama (1991, 2010), people in Western cultures (North America in particular) view the self as an independent and autonomous entity that is inclined to attend to the self more than others and emphasizes unique dispositions or traits of the self. These cognitive styles lead to an independent view of the self in Western cultures that remain invariant across different social contexts. In contrast, people in East Asian cultures hold an interdependent view of the self that is sensitive to information related to significant others and emphasizes the fundamental connections between the self and others. The findings and theories related to cultural differences in self-concept raise many interesting questions for cognitive neuroscientists. Are these different self-construals mediated by distinct neurocognitive processes in Western and East Asian cultures? How do cultures interact with biological factors such as genes to shape human brain mechanisms involved in self-related processing? In addition, our sensory experiences provide a basis for awareness of one's own existence. Thus, it is important to understand whether and how neural mechanisms underlying self-related processing are modulated by individuals' sensory experiences. During the past decade, brain imaging studies exploring these questions have strengthened our understandings of the neurocognitive processes related to the self and have greatly contributed to the development of cultural neuroscience. This chapter reviews recent neuroimaging studies that explore how the neural correlates of reflection on the self are influenced by cultural contexts, sensory experiences, and genetic makeup. The findings in this line of research improve our understanding of how the human brain reflects on the self and what emotional responses occur as a result of self-reflection.

## Cultural Experience and Neural Correlates of Self-Reflection

Regardless of the cultural differences in self-concept, it is commonly acknowledged that a human mind can reflect on the entity that possesses that mind; this is what neuroimaging studies refer to as self-reflection. A healthy adult can effortlessly report his or her own personality traits, social roles, and physical attributes. Is there neural activity in the human brain that is specific to self-reflection? Are similar neural activities engaged during reflection on different dimensions of one's own attributes? Do people from different cultures engage similar neural mechanisms underlying self-reflection? These are the questions that previous social/cultural neuroscience research aimed to address.

An early functional magnetic resonance imaging (fMRI) study explored the neural correlates of self-reflection on personality traits using the self-referential task (Kelley et al., 2002). Participants, who were recruited from a local community in the United States, were scanned using fMRI when they made judgments about trait adjectives related to the self ("Does this adjective describe you?") and a well-known public figure or a celebrity ("Does this adjective describe current U.S. President George Bush?"). A case judgment ("Is this adjective printed in uppercase letters?") was also included to control for perceptual processing and motor responses. It was found that blood oxygen level-dependent (BOLD) signals in the left inferior frontal and anterior cingulate cortex (ACC) increased significantly during personality trait judgments compared to case judgments. Moreover, the ventral medial prefrontal cortex (mPFC) was activated when comparing self versus celebrity judgments. Because self and celebrity judgments were matched in either perceptual or semantic processing, the ventral mPFC activation is believed to be engaged in self-referential processing during personality trait judgments.

What is the functional role of the ventral mPFC activation during trait judgments? Macrae, Moran, Heatherton, Banfield, and Kelley (2004) scanned American participants during the self-referential task. Participants were also given a surprise recognition memory test after scanning. During the memory test, participants were shown a number of trait adjectives that were previously presented during scanning along with an equal number of new trait adjectives. Participants had to indicate whether they remembered the word with high or low confidence or whether the word was new. Macrae et al. reported two interesting findings. First, the analysis of the fMRI data during the self-referential task revealed that contrasting trait adjectives that were remembered versus forgotten during the memory test showed activations in the ventral mPFC. Second, trait adjectives judged as being self-descriptive versus not during trait judgments also activated the mPFC. Ma and Han (2011) further showed that the increased ventral mPFC activity during self versus celebrity judgments was associated with the memory performances in the latter memory test such that greater ventral mPFC activity predicted higher recognition scores of the words used during self judgments. Consistent with these findings, it has been proposed that the ventral mPFC activity is engaged in the encoding of self-relevance of stimuli (Han & Northoff, 2009; Northoff et al., 2006), and the increased ventral mPFC activity reflects elaborated encoding of trait adjectives that leads to better performance during retrieval of these words.

Although the ventral mPFC activity associated with the self-referential processing has been observed in participants from different cultures, it remains unclear how the ventral mPFC activity is modulated by individuals' cultural experiences. According to Markus and Kitayama (1991, 2010), relative to East Asian cultural experiences, Western cultural practices, which facilitate self-identity in terms of inner qualities and encourage focus on one's own attributes, may enhance encoding of self-related stimuli and thus result in stronger ventral mPFC during self-reflection. In contrast, relative to Western cultures, individuals from East Asian societies construct self-identity with more emphasis on social relations and others' thoughts. Thus, East Asian cultural practices may lead to the engagement of brain regions involved in the processing of others' thoughts and beliefs during self-reflection.

To test these hypotheses, Ma and colleagues (2014b) scanned both Chinese and Danish participants, using fMRI, during self-reflection. Because China is a country characterized by a high interdependent cultural value (Li, Zhang, Bhatt, & Yum, 2006) and Denmark is a country dominated by a cultural value of independence (Thomsen, Sidanius, & Fiske, 2007), Ma et al. recruited Chinese and Danish participants from Beijing, China, and Aarhus, Denmark, respectively. This allowed them to examine whether and how different cultural practices in a Western culture and an East Asian culture shape the neural correlates of self-reflection. In addition, according to William James (1950), self-concept consists of different dimensions, such as social roles, personality traits, and physical attributes. Thus, Ma et al. examined whether brain activities engaged in different aspects of self-concept are influenced by cultural experiences in a similar vein. Chinese and Danish participants were asked to judge whether trait adjectives (e.g., "diligent" and "talkative") or words/phrases regarding physical features (e.g., "curly hair" and "wrinkled") or social roles (e.g., "tenant" and "professor") could be used to describe themselves or a familiar celebrity in their own culture. Individuals' cultural values regarding self-construals (i.e., interdependence) were measured using the Self-Construal Scale (Singelis, 1994) after scanning. This allowed them to test whether cultural group differences in neural correlates of self-reflection, if any, were mediated by the cultural value of interdependence.

Three interesting findings were reported by Ma et al. (2014b). First, the self-construal measure showed greater endorsement of the cultural value of interdependence in Chinese than in Danish participants. This suggests a reliable cultural value difference between participants from the two societies. The neuroimaging results revealed that contrasting self versus celebrity judgments on social roles, personality traits, and physical attributes similarly activated the ventral mPFC in both cultural groups (Figure 13.1A). However, the ventral mPFC activity in response to self versus celebrity judgments was significantly greater in Danish compared to Chinese participants, and the cultural group difference in the ventral mPFC activity was evident regardless of whether participants performed judgments on mental, physical, or social attributes (Figure 13.1B). Moreover, self-reflection on social roles significantly activated the temporoparietal junction (TPJ) in Chinese but not in Danish participants. The TPJ is involved in understanding others' beliefs (Saxe & Kanwisher, 2003), and lesions to this region produce mentalizing impairments (Samson, Apperley, Chiavarino, & Humphreys,

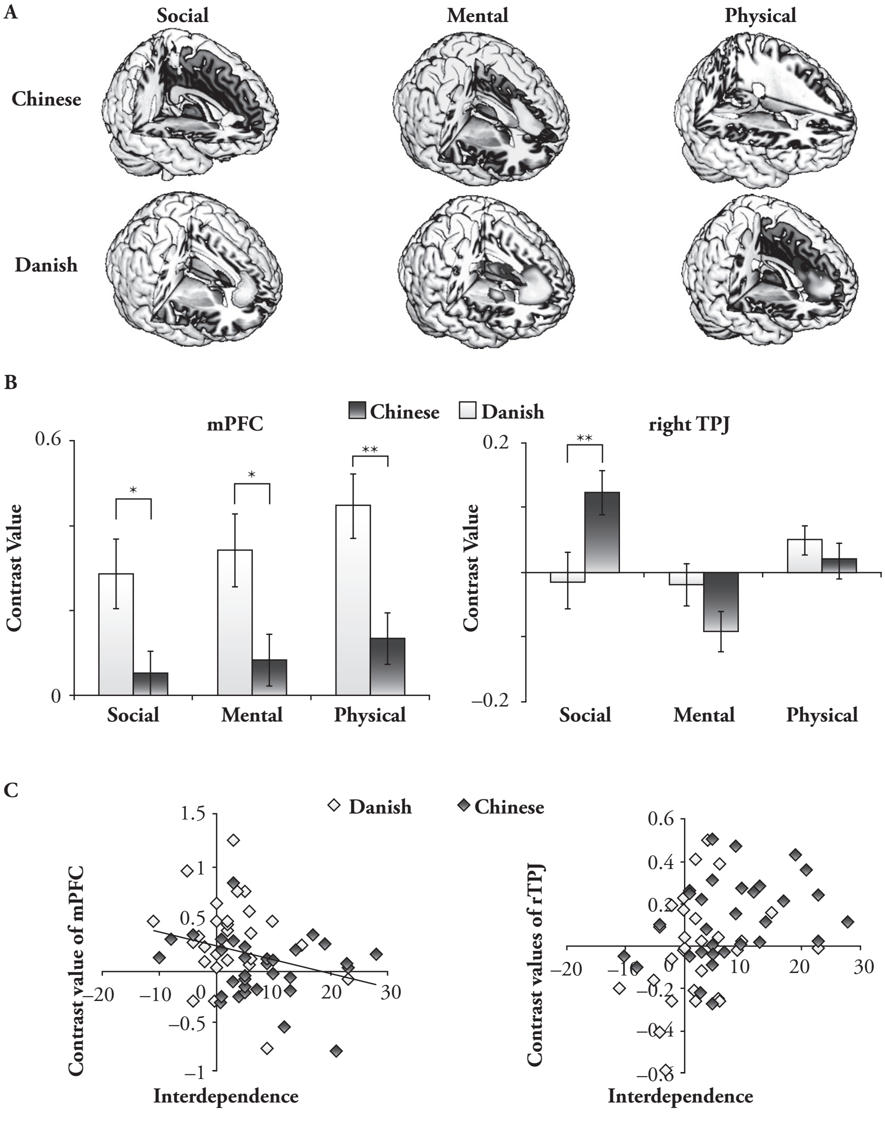

**Figure 13.1** (A) Brain activation in the contrast of self versus celebrity judgments on social, mental, and physical attributes. (B) Cultural group differences in the mPFC and TPJ activities associated with self versus celebrity judgments on social, mental, and physical attributes. (C) The correlations between the measure of interdependent and mPFC/TPJ activities involved in self-reflection on social attributes.

Source: Derived from Figures 1, 2, and 4 in Ma et al. (2014b).

2004). A regression analysis of all the participants revealed a significant negative correlation between the right TPJ and ventral mPFC activity associated with self-reflection on social attributes, consistent with the opposite pattern of ventral mPFC and TPJ activity in the two cultural groups. Moreover, a psychophysiological interaction analysis revealed that the functional connectivity between the ventral mPFC and the bilateral TPJ associated with self-reflection on social attributes was significantly stronger in Chinese than in Danes. These findings demonstrate different patterns of neural activity in the mPFC and TPJ recruited during self-reflection between the two cultural groups.

Second, if the cultural group differences in the neural correlates of self-reflection are associated with cultural value differences between Chinese and Danish participants, one may expect variations in the neural activity involved in self-reflection as a result of cultural value of interdependence at the individual level. Indeed, when collapsing individuals from the two cultural groups, Ma et al. (2014b) showed that individuals' interdependence scores were negatively correlated with ventral mPFC activity engaged in self-reflection on social attributes. In contrast, individuals' interdependence scores were positively correlated with the bilateral TPJ activity associated with self-reflection on social attributes (Figure 13.1C). Thus, the group and individual differences in the ventral mPFC and TPJ activities consistently support the notion that the neural activity underlying self-reflection varies across people with different cultural values of interdependence.

Third, Ma et al. (2014b) conducted a mediation analysis to further assess whether the cultural group differences in the brain activity involved in self-reflection were mediated by the cultural value of interdependence. They found that the measure of interdependence significantly mediated the relationship between the cultural affiliation (Chinese vs. Danish) and the TPJ activity involved in self-reflection on social attributes. The results of the mediation analysis indicate that the cultural group difference in the TPJ activity was partially explained by the difference in a cultural value—that is, interdependence of self-construal.

These neuroimaging findings have several implications regarding the relationship between sociocultural values and neural activities in key brain regions involved in self-reflection. First, a distributed neural network consisting of brain areas including the ventral mPFC and TPJ is engaged in the neurocognitive processing of information about the self. However, whether the TPJ is engaged in self-reflection depends on both the content of self-reflection (i.e., social attributes) and individuals' cultural experiences. The TPJ activity observed by Ma et al. (2014b) suggests that Chinese may take others' perspective when reflecting on their own social attributes because the TPJ supports inference of others' mental states (Saxe & Kanwisher, 2003). Second, brain activity involved in self-reflection may also vary as a function of cultural values held by individuals from the same culture. Cultural values of interdependence give rise to the distinct pattern of brain activity involved in self-reflection both between the two cultural groups and across individuals. Finally, generally speaking, distinct strategies of self-reflection in different cultures may be implemented by increasing the weight of a specific node in the neural circuit when processing self- or other-related information. The distinct patterned neural activity during self-reflection found between Chinese and Danish participants may correspond to the distinct self-concepts in East Asian and Western cultural contexts.

Cultural differences in neural correlates of self-reflections are not limited to those observed between Western and East Asian cultures. Religious beliefs also influence the neural correlates of self-reflection (Han et al., 2008, 2010). For example, Han et al. (2008) scanned nonreligious and Christian Chinese participants while they performed personal trait judgments on the self and a celebrity. They first showed that contrasting self versus celebrity judgments activated the ventral region of the mPFC (Talairach coordinates $x/y/z$ = 2/53/7) in nonreligious participants, replicating the findings of previous studies (e.g., Kelley et al., 2002; Zhu, Zhang, Fan, & Han, 2007). However, contrasting self versus celebrity judgments activated the dorsal (Talairach coordinates $x/y/z$ = 8/27/35 and –6/32/24) but not the ventral mPFC in Christian participants (Figure 13.2). The dorsal

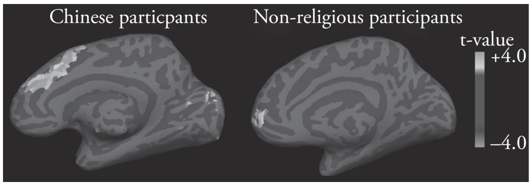

**Figure 13.2** The mPFC activity underlying self versus celebrity judgments on personality traits in Christian and nonreligious participants.

Source: Derived from Figure 2 in Han et al. (2008).

mPFC is engaged during reappraisal and evaluation of self-related stimuli (Northoff et al., 2006) and involved in inference of others' mental states (Ge & Han, 2008; Grèzes, Frith, & Passingham, 2004; Mitchell, Banaji, & Macrae, 2005;). Han et al. (2008) suggested that a religion (e.g., Christianity) that underscores the evaluative process of the self by God results in the engagement of the dorsal mPFC and weakens the process of encoding self-relevance in the ventral mPFC. Taken together, these neuroimaging findings provide evidence that the neural mechanisms of self-referential processing can be different between human communities within distinct sociocultural experiences, reflecting the neural consequences of divergent cognitive strategies during self-reflection in different cultures.

## Culture and Overlapping Neural Representation of the Self and Close Others

Markus and Kitayama's (1991, 2010) model of differences in self-construals between Western and East Asian cultures predicted an overlapping neural representation of the self and close others in the mPFC in East Asian participants but not in the Western participants. This prediction was tested by Zhu and colleagues (2007), who scanned both English-speaking Westerners and Chinese. Similar to previous studies, Zhu et al. asked participants to reflect on personality traits of themselves and a celebrity. A critical condition was included—that is, to reflect on personality traits of a close other (i.e., mother). The critical connection to Markus and Kitayama's model is the overlapping of mPFC activity in Chinese (interdependent) but not in Westerners (independent) during reflection on the self and one's mother.

Zhu et al. (2007) found that the contrast of self versus celebrity judgments on personality traits activated the ventral mPFC in both Chinese and Westerners. Thus, coding self-relevance of stimuli similarly engages the ventral mPFC in both cultural groups, although Zhu et al. did not directly compare the mPFC activity related to self-reflection between Chinese and Westerners. This is similar to the results reported by Ma et al. (2014b). However, the contrast of mother versus celebrity judgments on personality traits revealed significant activations in the ventral mPFC in Chinese but not in Westerners. In addition, if overlapping mPFC activity is engaged in reflection on the self and mother, one would expect an absence of activation in the contrast of self versus mother judgments. In contrast, if no overlapping mPFC activity is activated by self and mother judgments, one would expect greater activations when contrasting self versus mother judgments. This is indeed what Zhu et al. observed: The contrast of self versus mother judgments showed significant mPFC activation in Westerners but not in Chinese. These neuroimaging findings suggest that the Western independent self is dissociated from close others in the brain, whereas the East Asian (e.g., Chinese) interdependent self results in shared neural representation in the mPFC of oneself and one's mother. Later research (Wang et al., 2012) further showed that the neural representation of close others may vary as a function of their closeness to the self. Reflection on personality traits of one's mother induced greater activity in the mPFC relative to reflection on personality traits of one's father and best friend in Chinese participants. Such distinct neural representations of mother, father, and best friend in Chinese may arise from one's different daily experiences with the close others.

Ng, Han, Mao, and Lai (2010) further examined the causal relationship between culture and neural correlates of reflection on the self and close others using a cultural priming paradigm. In this paradigm, bicultural participants living in Hong Kong were exposed to Chinese or Western cultural icons as cultural primes. According to the dynamic constructivist model of culture (Hong, Morris, Chiu, & Benet-Martinez, 2000), people who have been exposed to multiple cultures may acquire multiple sets of cultural knowledge. Moreover, exposing individuals to cultural symbols may activate specific cultural knowledge, resulting in mindsets and behaviors that are consistent with that culture. Thus, one may predict that priming Chinese culture should facilitate overlapping neural representation of the self and close others in the mPFC, whereas priming Western cultures should enhance dissociation between neural representations of the self and close others. Indeed, Ng et al. found that Chinese cultural priming increased the mPFC activity associated with trait judgments of one's mother, whereas Western cultural priming produced the opposite effect. These findings are consistent with Zhu et al.'s (2007) findings of differential mPFC activity underlying reflection on mother's personality traits between Chinese and Westerners. In addition, the results indicate dynamic variations of the neural correlates of reflection on the self and close others and provide evidence for a causal effect of culture on the mPFC activity involved in self-reflection.

In summary, both cultural group comparison and cultural priming studies suggest that cultural values and practices not only modulate the neural correlates of self-reflection but also shape the neural correlates of reflection on close others. Similar cultural experiences of a population may result in a common neurocognitive process of self-reflection shared by individuals in a society. This, however, does not exclude the fact that individuals from a cultural group may be prone to one or another neurocognitive process during self-reflection given their distinct personal experiences, socioeconomic status, biological heredity, and so on. Note that transcultural neuroimaging studies that compare brain activities from two cultural group are challenged by the fact that two cultural populations are different in many respects. This is why future cultural neuroscience research should focus on whether or not observed group differences in brain activity are mediated by a specific cultural value. In addition, studies using cultural (self-construal) priming may help to examine a causal relationship between a cultural value and brain activity involved in a specific social cognitive process. Finally, similar to many psychological concepts that may have different meanings in different societies (Turner, 2012), the concept of self is also understood in different ways by different cultural populations. Future cultural neuroscience research should help to clarify the meaning of the self from the neuroscience perspective.

## Sensory Experience and Neural Correlates of Self-Reflection

It has been noted since Gibson (1979) that a key function of sensory perception is to distinguish between self and nonself. The aforementioned neuroimaging studies found that the neural correlates of self-reflection are sensitive to individuals' cultural experiences. However, it remains unclear whether and how sensory experiences influence neural representation of the self. Neuroimaging studies of blind individuals have shown that sensory experiences influence the functional organization of the brain profoundly. Studies of congenital blind adults have shown that the occipital cortex, which is typically involved in visual processing in sighted humans, is activated by heard sounds/words (Burton, Snyder, Diamond, & Raichle, 2002; Gougoux et al., 2009) and by Braille reading in blind individuals (Büchel, Price, Frackowiak, & Friston, 1998; Burton et al., 2002). Thus, the functional role of the occipital cortex strongly depends on sensory experiences.

In sighted people, visual input dominates information from other modalities and influences how they define the primitive sense of self, such as knowing that the self is the agency of one's own actions or the self owns one's body parts (Botvinick & Cohen, 1998; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). Such primitive sense of self provides a fundamental basis for interactions between the self and environments. Is the primitive sense of self provided by visual perception necessary for the neural correlates of self-reflection on personality traits? To address this issue, we scanned sighted individuals during reflection on personality traits of the self and a celebrity (Ma & Han, 2011). Valence (positive vs. negative) judgments on trait adjectives were also included to control for semantic processing and motor responses. The contrasts of self versus celebrity judgments on trait adjectives, which were presented via either an LCD projector onto a rear projection screen or through an MR-compatible pneumatic headphone system, were calculated respectively to examine the effect of sensory input on the mPFC activity involved in self-reflection. Interestingly, we found that self versus celebrity judgments on visually presented trait adjectives significantly activated the ventral mPFC (Figure 13.3A). Moreover, a psychophysiological interaction analysis revealed that the functional connectivity between the ventral mPFC and occipital cortex was significantly increased during self compared to celebrity judgments on visually presented trait adjectives. In contrast, the ventral mPFC did not show significant activation during self versus celebrity judgments on aurally presented trait adjectives. The contrast of celebrity versus valence judgments on trait adjectives delivered through either visual or auditory modality similarly activated the dorsal region of the mPFC. Thus, it seems that the ventral mPFC activity related to self-concept representation strongly depends on the input from the occipital cortex.

Ma and Han (2011) then tested whether the ventral mPFC activity underlying self-representation is taken over by the auditory modality in blind individuals for whom the auditory rather than the visual inputs dominate the distinction between self and nonself. The authors scanned congenital blind adults and sighted controls while they performed self and celebrity judgments on aurally presented trait adjectives. Unlike the sighted controls, who did not show ventral mPFC activation in the contrast of self versus celebrity judgments, blind individuals showed significantly increased ventral mPFC activity during self-reflection (Figure 13.3B). Moreover, self-judgments caused increased functional connectivity between the

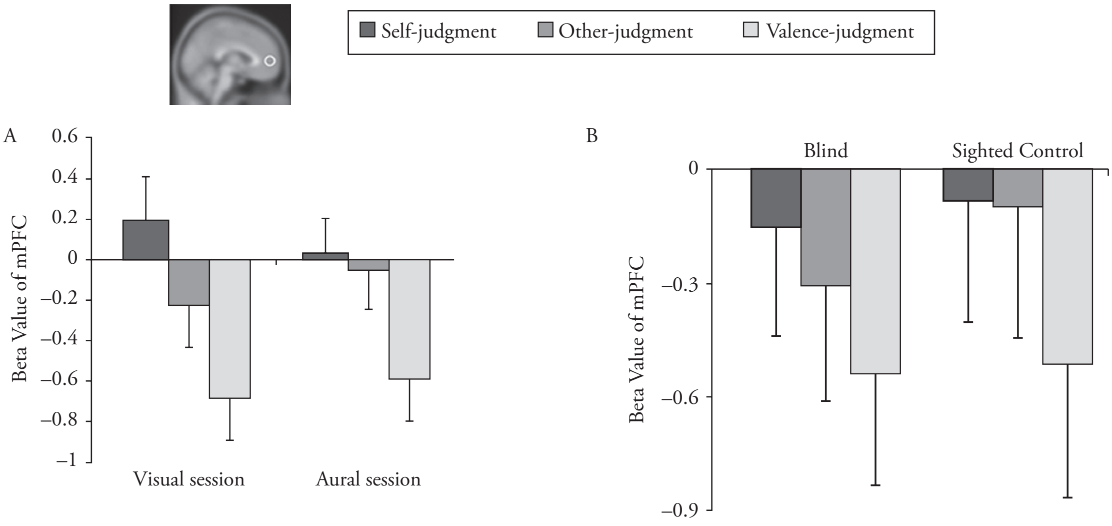

**Figure 13.3** (A) The signal intensity in the mPFC during trait or valence judgments on trait adjectives that were visually presented in sighted individuals. (B) The signal intensity in the mPFC during trait or valence judgments on trait adjectives that were aurally presented in sighted and blind individuals.

Source: Derived from Figures 2 and 4 in Ma and Han (2011).

ventral mPFC and the bilateral occipital cortex in blind participants, similar to that observed in sighted individuals who performed judgments on visually presented trait adjectives. Therefore, the neuroimaging results from sighted and blind participants indicate that it is sensory experience rather than visual or aural modality per se that is critical for the development of neural correlates of self-reflection in the ventral mPFC. The frontal activity underlying self-reflection of personality traits depends on the sensory experiences that produce the primitive sense of the self.

## Genetic Influences on Neural Correlates of Self-Reflection

Although the previous studies found evidence for distinct neural correlate of self-reflection between subject groups who had different cultural or sensory experiences, these studies also observed individual differences in neural activities underlying self-reflection even in the same cultural group. This raises the question of whether and how biological factors such as genes, in addition to cultural environments, modulate the neural mechanisms underlying self-reflection. Although the self is usually defined in terms of others and self-concept is thought to be a social construct (e.g., Turner, Oakes, Haslam, & McGarty, 1994), the brain that underlies self-reflection is a biological organ per se. Thus, the neural correlates of self-reflection in the brain may undergo genetic influences.

To address this issue, Ma and colleagues (2014a, c) tested the effect of a candidate gene—that is, the serotonin transporter promoter polymorphism (*5-HTTLPR*)—on the neural correlates of self-reflection. *5-HTTLPR* is composed of a short and a long version that result in differential 5-HTT expression and function (Canli & Lesch, 2007). The short allele of *5-HTTLPR* has been recognized as a risk allele for depression and anxiety (Lotrich & Pollock, 2004). Short allele carriers exhibit stronger amygdala activity to negative environmental stimuli relative to homozygous long variant (l/l) (Canli et al., 2005; Hariri et al., 2002). Given that cognitive styles in depression are characterized by negative views about oneself, environment, and future in depression (Beck, Rush, Shaw, & Emery, 1979), it is possible that self-reflection in short allele carriers with high risk for depression and anxiety may either engage different neural mechanisms or produce different emotional consequences compared to those in l/l carriers.

Ma et al. (2014a, 2014b) scanned Chinese adults with s/s or l/l variants of *5-HTTLPR*, using fMRI, during reflection on personal attributes of oneself and a celebrity. The initial analysis of the fMRI data from the two genotyped groups revealed similar mPFC activations in the contrast of self versus celebrity judgments in both s/s and l/l genotypes (Figure 13.4A) (Ma, 2012). The comparison between the mPFC activities in s/s and l/l carriers did not find significant differences. Thus,

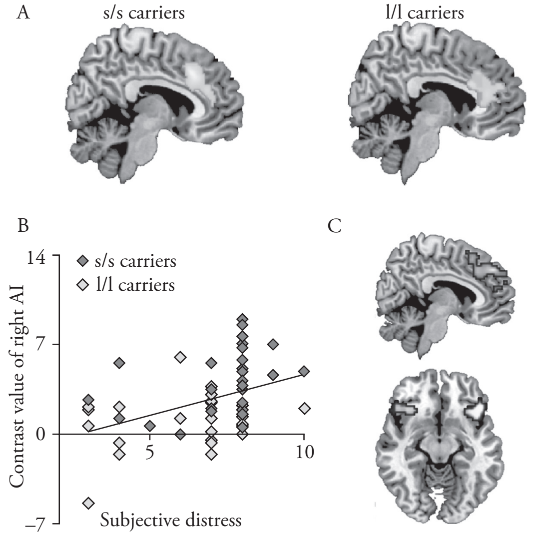

**Figure 13.4** (A) The mPFC activity during self versus celebrity judgments on personality traits in s/s and l/l allele carriers of 5-HTTLPR. (B) The correlation between the right anterior insular activity and subjective distressed feelings induced by negative self-reflection. (C) Relative to l/l, individuals with the s/s genotype showed stronger activation in the dorsal ACC and the right anterior insula (AI) induced by negative self-reflection.
Source: Derived from Figure 1 in Ma et al. (2014a).

it seems that *5-HTTLPR* does not modulate the neural activity-related encoding of self-relevance of stimuli during self-reflection on personality traits. However, the analysis focusing on negative self-reflection revealed significant *5-HTTLPR* effect on the neural activity. In a slightly different design, Ma et al. (2014a) asked participants to rate on a 4-point Likert scale whether positive or negative trait adjectives could describe the self (1 = not at all like me; 4 = very much like me). Trait adjectives that were rated high self-relevant (rating scores of 3 or 4) or low self-relevant (rating scores of 1 or 2) were modeled separately. Rating negative trait adjectives as high self-relevant is similar to rating positive trait adjectives as low self-relevant in the sense of acknowledging one's own undesired attributes. Thus, the contrast of negative (high – low self-relevance) versus positive (high – low self-relevance) was calculated to identify brain activity related to negative self-reflection that was independent of influences of perceptual/semantic processing and motor responses. Interestingly, this contrast identified significant activations in the anterior cingulate and bilateral insular cortices across all subjects. Moreover, a regression analysis showed that individuals who felt more distressed when thinking about their own negative traits activated the bilateral anterior insula more strongly during negative self-reflection (Figure 13.4B). Thus, the anterior insular activity was associated with distressed feelings induced by negative self-reflection. More interesting, a whole-brain two-sample *t*-test revealed that, relative to l/l, s/s genotype participants showed greater activity in the anterior cingulate and right anterior insular cortices during negative self-reflection (Figure 13.4C). Separate analyses further confirmed that the anterior cingulate and insular activities associated with negative self-reflection were significant in s/s but not l/l carriers. In a control experiment, Ma et al. (2014a) also asked s/s and l/l carriers to reflect on personality traits of a close friend. Similar analyses did not show any activation associated with reflection on a friend's negative traits in either s/s or l/l carriers. Thus, the genetic influences on negative reflection were specific to the self.

In a following study, Ma and colleagues (2014b) further examined whether *5-HTTLPR* affects the association between self-construals and the neural activity involved in self-reflection of personality traits by scanning s/s and l/l carriers during reflection of personal attributes of oneself and a celebrity. They found that although s/s and l/l genotype groups did not differ significantly in interdependence of self-construals, the relationship between self-construal scores and neural responses to self-reflection was moderated by *5-HTTLPR*. Specifically, the l/l but not the s/s genotype group showed significant association between self-construals and activity in the social brain network consisting of the mPFC, bilateral middle frontal cortex, TPJ, insula, and hippocampus during self-reflection on personality traits.

The findings of imaging genetics suggest two patterns of genetic modulation of the neural correlates of self-reflection. First, *5-HTTLPR* modulates the activation in the anterior cingulate and anterior insula associated with affective components (e.g., distressed feelings) of self-reflection but not in the mPFC linked to the cognitive components (e.g., the encoding of self-relevance) of self-reflection. This is different from the cultural influences on the neural correlates of self-reflection that is mainly manifested in the mPFC. Second, *5-HTTLPR* moderates the relationship between cultural values (i.e., interdependence) and the neural activity involved in self-reflection. This finding suggests a possible way of gene × culture interaction on human brain and mind; that is, the association between a cultural trait and brain activity involved in self-reflection is constrained by a specific genetic polymorphism.

## Self-Reflection and Mental Health

According to the World Health Organization, mental health is a state of well-being in which an individual can realize his or her own abilities, cope with the normal stresses of life, work productively and fruitfully, and make contributions to his or her community. Therefore, how one thinks about the self plays a key role in mental health. Indeed, a positive view of the self, either explicit or implicit, makes one feel good, and the human desire to view the self positively is of fundamental importance (James, 1890/1950). Seeking positive self-views provides a fundamental ground of one's own existence and facilitates mental health (Myers & Diener, 1995). In contrast, to associate the self with negative characters can induce activation of the neural circuits that produce distressed feelings (e.g., Ma et al., 2014a). An overladen negative view of the self may even lead to mood disorders such as depression (Beck et al., 1979).

Cultural neuroscience studies of self-related processing have implications for understanding mental health and mood disorder that may vary across different cultural contexts. For example, if faster behavioral responses to one's own face compared to others' faces (i.e., self-face advantage) reflect implicit positive views of the self (Ma & Han, 2010), greater self-face advantage in British compared to Chinese participants (Sui et al., 2009) thus suggests that Western cultures may give rise to stronger positive self-views relative to East Asian cultures. Moreover, the finding that self-face recognition is more susceptible to the influence of viewing significant others in Chinese than in American individuals (Liew et al., 2011; Ma & Han, 2009) implicates that positive self-views may be more easily dampened by others in East Asian than in Western cultures. The transcultural neuroimaging findings are consistent with this analysis because Chinese culture promotes neurocognitive processes of taking others' perspective during self-reflection on social attributes, whereas Danish culture does not seem to do so (Ma et al., 2014b). Thus, future research of mental health may take into account the cultural neuroscience findings of self-reflection to investigate whether the same neurocognitive mechanisms mediate psychiatric disorders across cultures. Future research should also examine how genes interact with cultures to influence mental health because genes (e.g., *5-HTTLPR*) apparently modulate the neural correlates of self-reflection and consequential emotional responses (Ma et al., 2014a). Moreover, behavioral studies have provided evidence that culture may interact with genes to influence strategies for coping with stress (Kim et al., 2010) and that cultural values may buffer genetically susceptible populations from increased prevalence of affective disorders (Chiao & Blizinsky, 2010). Taking into account both cultural and genetic influences on mental health helps us to understand differences in emotion and mood disorders between different populations and across individuals.

## Conclusions

Cultural neuroscience studies have uncovered how the neural correlates of self-reflection are modulated by cultural/sensory experiences and genes. The findings reviewed in this chapter provide a neuroscience framework for understanding whether and how self-reflection may vary across different cultural groups and across individuals with different cultural values and genetic makeup. The findings of cultural neuroscience studies suggest that cultural experiences affect the brain activity associated with the cognitive dimension of self-reflection (e.g., coding self-relevance or taking others' perspective). Sensory experiences determine whether the mPFC is engaged in self-reflection of trait adjectives that are delivered through the dominant sensory (e.g., visual vs. auditory) modality. An individual's genetic makeup (e.g., *5-HTTLPR*) modulates the brain activity underlying distressed feelings produced by negative self-reflection and moderates the association between cultural value (e.g., interdependence) and brain activity engaged in self-reflection. These findings indicate that the neural cognitive/affective processes involved in self-reflection are strongly influenced by sociocultural and biological factors.

Cultural neuroscience studies of self-reflection and other neurocognitive processes have uncovered the biosocial nature of the human brain (Han & Northoff, 2008; Han et al., 2013). These findings reveal how the functional organization of the human brain is essentially driven by genes and sociocultural experiences in order to fit into a specific society. The specific pattern of neural activity underlying self-reflection arising from one's sociocultural experiences may accommodate an individual to his or her social environment and reduce the conflict between the self and other during social interactions. Cultural neuroscience researchers should extend their work to the investigation of abnormal individuals so as to clarify whether there is culturally specific neural activity underlying mental disorders. This research may lead to the production of culturally specific treatments for mental problems.

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CHAPTER

14

# Identifying a Cultural Resource: Neural Mechanisms Underlying Familial Influence on Adolescent Risk Taking

Eva H. Telzer, Andrew J. Fuligni, *and* Adriana Galván

## Abstract

Family obligation, which implies children's role in the support and assistance of their family, is a fundamental aspect of family life. Family obligation has important implications for the adjustment of adolescents from Mexican backgrounds, relating to lower levels of risky behavior. Risk taking underlies many behavioral and health factors, such as substance use and externalizing behavior, that contribute to the public health burden during the adolescent period. Advances in developmental neuroscience have identified key neurobiological underpinnings of adolescent risk taking, but there is little understanding of how these neural processes interact with cultural and social processes to promote or prevent risk taking. We present a multimethod, longitudinal program of research that uses self-reports of risk taking and substance use, experimental tasks, and functional magnetic resonance imaging to examine the mechanisms by which a culturally meaningful type of family relationship—family obligation—buffers Mexican youth from drug use and risk taking.

**Key Words:** cultural resource, family, adolescent risk taking, neuroscience, longitudinal

Family obligation, which implies children's role in the support and assistance of their family, is a fundamental aspect of family life. Family obligation has important implications for the adjustment of adolescents from Mexican backgrounds, relating to lower levels of risky behavior. Risk taking underlies many behavioral and health problems, such as substance use and externalizing behavior, that contribute to the public health burden during the adolescent period. Recent advances in developmental neuroscience have identified key neurobiological underpinnings of adolescent risk taking, but there is little understanding of how these neural processes interact with cultural and social processes in order to promote or prevent risk taking. In this chapter, we present a multimethod, longitudinal program of research that uses self reports of risk taking and substance use, experimental tasks, and functional magnetic resonance imaging (fMRI) to examine the mechanisms by which a culturally meaningful type of family relationship—family obligation—buffers Mexican youth from drug use and risk taking.

## Risk Taking and Drug Use in Adolescence

Adolescence is a time of heightened propensity for risk taking, impulsivity, and reckless behavior that often lead to poor decisions such as drug initiation (Arnett, 1992; Chambers, Taylor, & Potenza, 2003; Steinberg, 2008). Adolescent drug use is one of today's most important social concerns because it contributes to a host of serious immediate and long-term problems, such as risky sexual behavior, incarceration, morbidity and mortality, violent behavior, and high school drop out (Ellickson, Bui, Bell, & McGuigan, 1998; Fergusson, Horwood, & Swain-Campbell, 2002; Guy, Smith, & Bentler, 1994; Kann et al., 1998; Lancot & Smith, 2001; Ramirez et al., 2004). These consequences are of particular concern during high school, a critical time for drug use initiation and experimentation. By the time youth reach 12th grade, 47% have tried an illicit drug at least once (Johnston, O'Malley, Bachman, & Schulenberg, 2009).

Challenges associated with immigration, discrimination, and socioeconomic disparities place adolescents from Mexican backgrounds at a greater risk for a variety of adjustment problems, including substance use. Compared to other ethnic groups, Latino teenagers begin using drugs at an earlier age, show greater risk for developing drug use disorders in adulthood due to early drug use onset, and have higher overall rates of illicit drug use (Centers for Disease Control and Prevention, 2006; Ellickson, Martino, & Collins, 2004; Gil, Wagner, & Tubman, 2004; Johnston et al., 2009; Vega, Zimmerman, Warheit, Apospori, & Gil, 1993). In particular, Latinos have the highest rate for the most dangerous drugs, such as heroin, crack, and crystal methamphetamine (Johnston et al., 2009).

Drug use among Latinos is an especially important social concern because Latinos have become the largest ethnic minority group in the United States, comprising 16.3% of the US population, with those from Mexican backgrounds representing 63% of all Latinos in the United States (Ennis, Rios-Vargas, & Albert, 2011). Furthermore, in Los Angeles, California, the site of the current study, Latinos make up 48% of the population, with those from Mexican backgrounds representing 84% of Latinos in Los Angeles (Ennis, Rios-Vargas, & Albert, 2011). Attending to the health of this growing population should be a central concern and viewed as an investment in the health of the country (Ojeda, Patterson, & Strathdee, 2008). In order to address cultural disparities in substance use, there is great need for systematic research that examines cultural risk and protective factors for Latino youth who come from families that may possess beliefs and values that differ from the norms of American society. Given the higher rate of drug use among Latinos and the serious consequences of drug use, it is imperative to identify culturally relevant factors that can enhance the development of efforts to reduce drug use among this growing population.

## Culturally Important Family Relationships

The emphasis on the role of children and adolescents to support, assist, and take into account the needs and wishes of the family is perhaps the most distinctive aspect of family relationships among families from Mexican backgrounds in the United States. This type of family connection, often called "familism" or "family obligation," exists within Mexican and other Latin American families (Suárez-Orozco & Suárez-Orozco, 1995). Youth from these families stress the importance of spending time with the family, high family unity, family social support, and interdependence for daily activities (Cuellar, Arnold, & Gonzalez, 1995; Fuligni, 2001). When families immigrate to the United States, this tradition takes on a very real significance when parents face difficulty finding stable and well-paying employment and are unfamiliar with the norms of American society.

Compared to youth from European backgrounds, youth from Mexican backgrounds spend almost twice as much time helping their family each day, and they assist their family 5 or 6 days per week on average, suggesting that family assistance is a meaningful daily routine for these adolescents (Telzer & Fuligni, 2009a). Furthermore, young adults from Mexican backgrounds make financial contributions to their families at higher rates than their peers (Fuligni & Pedersen, 2002), and those from second and third generations continue to maintain a strong sense of family obligation (Fuligni, Tseng, & Lam, 1999).

One way to capture the meaning and importance of family obligation is to think of the family as a social identity. Thinking about the family as a social identity captures an aspect of family relationships that is often overlooked—a sense of "we-ness" that comes from being a member of a group. Such group membership is experienced through shared values, norms, and beliefs. According to social identity theory, identifying with a social group enhances one's willingness to support and assist that group and provides a sense of meaning, belonging, and well-being (Hogg, 2003). Indeed, adolescents who internalize the familistic values of their family feel more connected to and embedded within a supportive family network, which can provide them with a sense of support and structure to help them deal with the challenges associated with being a teenager in American society (Hardway & Fuligni, 2006).

The following quotes from teenagers who have participated in our research help to exemplify how family obligation is associated with a sense of connection to the family. A 15-year-old female adolescent from a Mexican immigrant family said the following:

> Sometimes my mom feels sick or she feels bad. We'll all come and help her, and I'll help her as well to clean the house. And my dad, when he really needs

> help working I'll, I'll go help him, and, well my family, sometimes they'll need someone to go help and I'll help, I'll go. I guess that just makes me feel more closer to the family.

This adolescent derives a sense of family cohesion from providing help to her family. Such cohesion can provide adolescents with a sense of connection and support, potentially increasing their willingness to talk to and share their experiences with their family. For example, a 15-year-old female from a Mexican-American family said the following about her father:

> He loves to be in the kitchen. And, that's how I help him out. I'm washing dishes before he starts cooking, he loves cooking in a clean kitchen. And I know that. So I'll go in and, like, start washing dishes. So, that's usually how we, like, we come together and just start talking.

By helping her father in the kitchen, this adolescent feels closer to her father and finds the time and space to talk to him. Thus, adolescents with greater family obligation values may feel stronger attachments to their family and use their family as a source of support and guidance (German, Gonzales, & Dumka, 2009), more willingly sharing their daily experiences with them (Yau, Taspoulos-Chan, & Smethana, 2009). Such disclosure may open up family discussions about appropriate behavior and strategies for dealing with peer pressure. Parents can provide advice and support, helping their child develop coping strategies to avoid risky behavior.

## Family Obligation and Adolescent Risk Taking

Family obligation values may be a cultural resource, protecting youth from substance use. To test this association, we examined the links between family obligation and substance use among 385 Mexican-origin adolescents in the 9th and 10th grades. Adolescents completed several self-report measures, including the Youth Risk Behavior Survey Questionnaire, a common measure of substance use that has been shown to be valid and reliable for Latino youth (Centers for Disease Control and Prevention, 1989; Kerr, Beck, Shattuck, Kattar, & Uriburu, 2003). Youth indicated the frequency with which they used substances in the past 30 days, including cigarettes, alcohol, marijuana, prescription drugs without a doctor's prescription, cocaine, crystal meth, and heroin. Youth also completed the family obligation values scale (Fuligni, Tseng, & Lam, 1999), indicating how often they felt they should assist with household tasks, spend time with their family, and consider their families' needs and wishes when making important decisions.

Our findings demonstrated the protective role of family obligation, such that Mexican-origin youth with higher family obligation values had lower rates of substance use, including lower cigarette, alcohol, marijuana, and cocaine/methamphetamine use (Figure 14.1; Telzer, Gonzales, & Fuligni, 2014). Although some prior research has highlighted the protective role that family obligation values play for adolescents' health risk behaviors (e.g., German et al., 2009; Gil, Wagner, & Vega, 2000; Kaplan, Napoles-Springer, Stewart, & Perez-Stable, 2001; Ramirez, et al., 2004; Romero & Ruiz, 2007; Unger et al., 2002), we know little about the mechanisms by which it is protective. We therefore examined potential mediators to explain the protective role of family obligation. We found that family obligation values were associated with lower levels of substance use because adolescents were less likely to associate with deviant peers and were more likely to disclose their activities to their parents. Deviant peer association and adolescent disclosure accounted for 37–100% of the original effect of family obligation values on substance use. Our findings suggest that Mexican adolescents' decisions to engage in substance use may depend on their cultural values; adolescents with stronger family obligation values

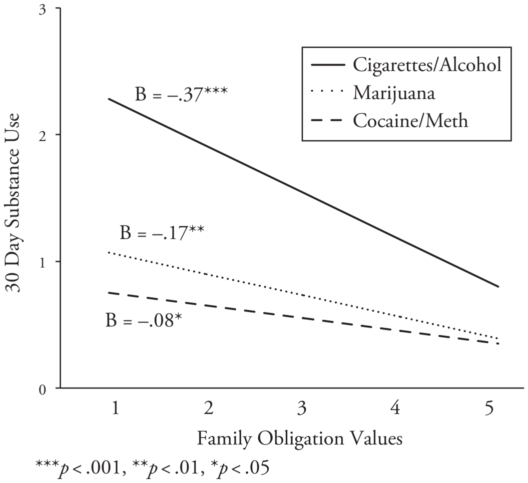

**Figure 14.1** Higher family obligation values relate to lower levels of cigarette/alcohol, marijuana, and cocaine/methamphetamine use. For alcohol/cigarettes, the *y*-axis ranges from 0 to 6, where 0 = 0 days and 6 = all 30 days in the past month. For marijuana, the *y*-axis ranges from 0 to 5, where 0 = 0 times and 6 = 100 or more times in the past month. For other illicit/prescription, the *y*-axis ranges from 0 to 5, where 0 = 0 times and 5 = 40 or more times in the past month.

engage in less substance use behavior because they are avoiding deviant peers and are opening up more to their parents.

These findings suggest that family obligation may reduce risky behavior in several ways. First, youth with stronger family obligation values may develop better decision-making skills. By putting their families' needs first and delaying personal gratification for the families' sake, these youth may develop more effective cognitive control, a skill necessary for avoiding deviant peers and health-compromising behaviors. Second, family obligation may make risk taking comparatively less rewarding. Youth with stronger family obligation values report more negative consequences for engaging in risk taking because it would reflect poorly on their whole family (German et al., 2009). Therefore, risk taking itself may be less salient and enticing. To test these potential explanations, we turned to fMRI to better understand the underlying neural mechanisms of family obligation and risk-taking behavior.

## The Neurobiology of Risk Taking During Adolescence

Evidence from developmental neuroscience suggests that risk-taking behavior increases during adolescence partly due to changes in the brain's neural circuitry (Casey, Jones, & Somerville, 2011; Steinberg, 2008). Subcortical regions, which comprise neural regions associated with the evaluation of rewards (e.g., amygdala and ventral striatum), mature functionally relatively early, leading to increased reward sensitivity during adolescence. In contrast, cortical regions, which comprise neural regions involved in higher-order cognition and impulse control (e.g., ventral and dorsal lateral prefrontal cortices), gradually mature over adolescence and into adulthood. The relative imbalance in the functional use of these systems (Figure 14.2A) is thought to leave the adolescent more vulnerable to take risks and less able to modulate social and emotional decisions (Casey et al., 2011; Steinberg, 2008). Immature cognitive control development relative to the reward system may hinder appropriate evaluation of risk and bias youth toward risky decisions.

Although risk taking can lead to problems, it can also be an adaptive and beneficial behavior, supporting the propensity for learning new skills. Risk taking may support the evolutionarily adaptive, goal-directed behavior that begins to emerge during adolescence (Crone & Dahl, 2012; Spear, 2000). Indeed, prior work has demonstrated the adaptive role of risky behavior (e.g., Humphreys, Lee, & Tottenham, 2013), with higher levels of risky, exploratory behavior associated with more mature white matter integrity in frontal-limbic circuitry in adolescence (Goldenberg, Telzer, Fuligni, Lieberman, & Galvan, 2015). Some aspects of risk taking may therefore be positive behaviors that lead to learning and benefits to youths' development. Nonetheless, when occurring within a health-compromising context, such as drug use, risky sexual behavior, or reckless driving, adolescent risk taking can be problematic.

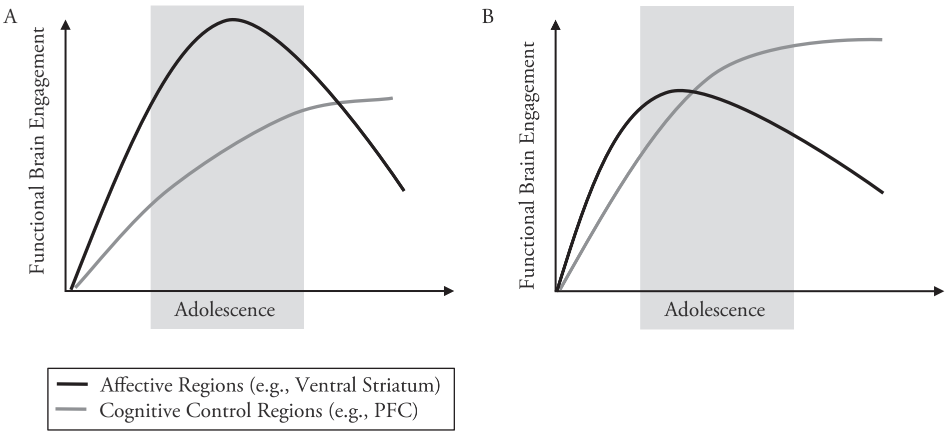

**Figure 14.2** (A) Dual systems model of adolescence. Neurobiological model depicting relatively earlier development of subcortical limbic regions (e.g., ventral striatum) relative to the protracted development of cognitive control regions (e.g., dorsolateral PFC). This neural imbalance in development is suggested to underlie risky decision-making behavior during adolescence. Note that the period of adolescence is depicted with a gray box. (B) Reducing the neural imbalance in adolescence. Family obligation is predicted to relate to reductions in reward sensitivity and to increases in cognitive control during adolescence.

Source: Panel A adapted from Casey et al. (2011).

The dual systems model of neurobiological development offers a promising way to view the maturational underpinnings of risk taking during the teenage years. However, risk taking does not occur in a social or cultural vacuum, and it is critical to examine how neural mechanisms interact with fundamental social and cultural processes during adolescence. We tested the hypothesis that this normative functional imbalance between cognitive and affective systems is reduced in youth with high family obligation values. If indeed family obligation is helping adolescents to make better decisions by engaging in more cognitive control and reducing the salience of risks, we predicted that it may be functioning by reducing the neural imbalance during adolescence by increasing cognitive control and reducing reward sensitivity (Figure 14.2B).

## Testing the Hypothesized Model of Family Obligation and Risk Taking

Our goal was to examine the links between family obligation, neural activation, and adolescents' risk-taking behaviors (Figure 14.3). By examining each of these links (cultural values → brain; brain → risk-taking behavior), we can gain a deeper understanding of how family obligation is processed in the developing brain and how these neural activations are associated with relevant behavioral changes. To test this, we examined the following:

1. Whether family obligation was associated with activation in neural regions involved in reward processing and whether this reward activation was associated with reduced risk-taking behavior
2. Whether family obligation was associated with reduced reward sensitivity during risk taking and whether this reduced reward activation was associated with reduced risk-taking behavior

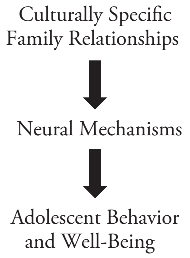

**Figure 14.3** Research strategy for testing the neural mechanisms that may underlie the association between cultural resources (e.g., culturally important family relationships) and adolescent behavior.

3. Whether family obligation was associated with increased activation in the PFC during cognitive control and whether this heightened cognitive control activation was associated with reduced risk-taking behavior

## Family Obligation and Reward Activation

We created a family obligation task modeled after the work of Moll and colleagues on charitable giving (Moll et al., 2006). During a functional brain scan, 40 Mexican-origin adolescents were presented with a series of financial offers that varied in terms of whether they represented gains or losses for the participants and their families. Noncostly-Reward trials gave participants the option to earn money without a cost to the family (e.g., YOU + \$3.00 FAM –\$0.00), whereas Costly-Donation trials gave participants the option to give money to their family at a cost to themselves (e.g., YOU –\$1.00 FAM + \$3.00). Participants and their families were paid in cash according to their choices on the task. We examined brain activation during the Costly-Donation and Noncostly-Reward trials, which allowed us to focus on neural activation when making a donation to the family that involves self-sacrifice, a behavior that most closely approximates family obligation behaviors. Costly-Donation trials were contrasted to pure cash gains for oneself, which have been shown to be a hedonistically rewarding experience that is associated with activation in the ventral striatum (Moll et al., 2006).

Consistent with our previous work (e.g., Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010; Telzer et al., 2011), we found that costly donation decisions to the family engaged the reward network. Although the ventral striatum was significantly active during both costly donation and noncostly reward decisions, decisions to contribute to the family engaged the ventral striatum more so than did personal noncostly reward decisions (Figure 14.4A). However, the extent of this activation varied depending on youth's family obligation values, showing that those with the strongest values had the greatest ventral striatum activation during costly donations toward their family (Figure 14.4B). These findings suggest that among Mexican youth who strongly value family obligation, decisions to make sacrifices for the family are meaningful, rewarding decisions. Thus, family relationships that are culturally meaningful provide adolescents with a sense of reward, and this reward may be protective and lead to positive, healthy outcomes.

To examine whether the rewarding nature of family obligation relates to youths' health risk behaviors, 32 of these adolescents were followed for 1 year after the scan session. Adolescents completed the Rule-Breaking subscale of the Youth Self-Report form of the Child Behavior Checklist (Achenbach, 1991). At the time of the scan and 1 year later, adolescents indicated whether they engaged in a range of risky behaviors, such as associating with deviant peers, lying, stealing, drinking alcohol without parental approval, using drugs, and skipping school. Results indicated that increased neural response in the ventral striatum during costly donations compared to noncostly reward trials was significantly associated with longitudinal decreases in risky behaviors (Figure 14.4C; Telzer, Fuligni, Lieberman, & Gálvan, 2013a). The more striatum activation youth showed when providing assistance to their family, the more their risk-taking behaviors decreased over the high school years. These data suggest that the meaningful and rewarding nature of family obligation is protective for Mexican-origin youth.

## Family Obligation and Neural Sensitivity to Risk Taking

To test how family obligation relates to reward activation during risk taking, we scanned 48 Mexican-origin adolescents as they engaged in a risk-taking task, the Balloon Analogue Risk Task (BART; Lejuez et al., 2002). On each trial of the task, participants are shown a virtual red-colored balloon and given the option to inflate the balloon, which can either grow larger or explode. The larger the balloon is inflated, the greater the monetary reward but the higher the probability of explosion. Participants press one of two buttons to either inflate (pump) the balloon or "cash out." Importantly, the probability of risk on each trial is unknown, much like risk taking in the real world. Participants received a payoff (25¢) for each pump on which the balloon was successfully inflated and could stop inflating the balloon at any point and keep the accumulated payoff. If the balloon exploded, the participant received no payoff for that trial, but earnings from previous trials were unaffected.

We examined how family obligation values were associated with risk taking and neural activation

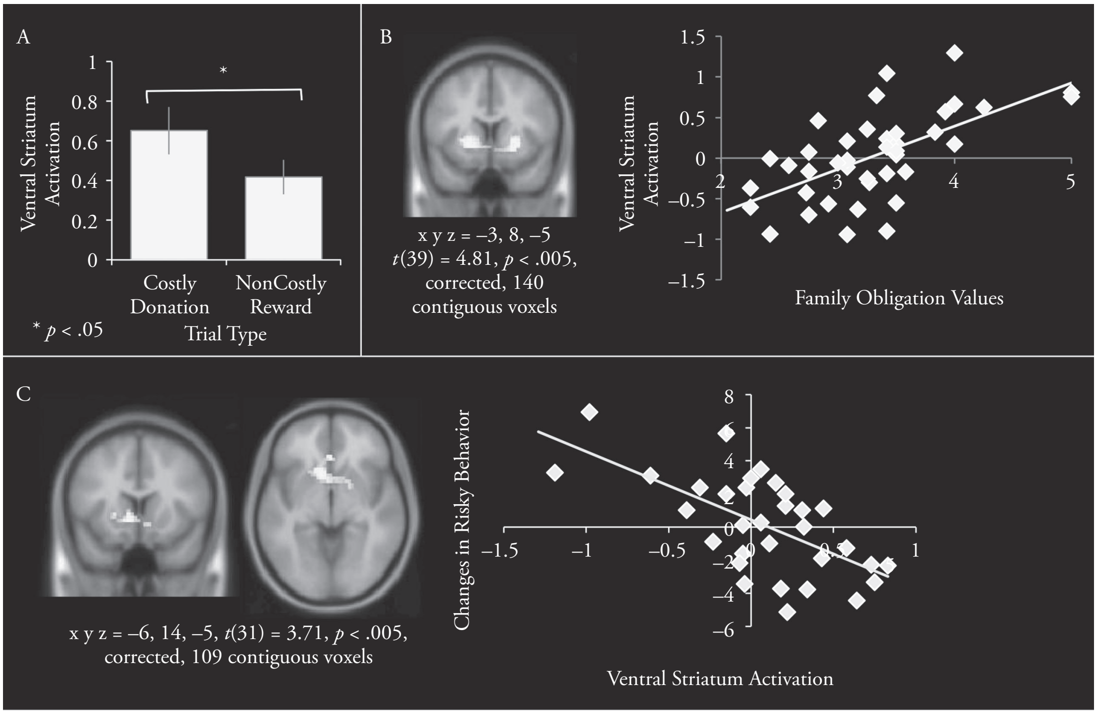

**Figure 14.4** (A) Ventral striatum (VS) activation during the family task. VS activation is greater to costly donation decisions than to noncostly reward decisions. (B) Greater family obligation values are associated with increased VS activation when contributing to the family compared to gaining personal monetary rewards. (C) Adolescents who show greater VS activation to costly donation decisions demonstrate longitudinal decreases in risk-taking behavior. Note that each axis titled "Ventral Striatum Activation" represents percentage blood oxygen level-dependent signal change in the ventral striatum to costly donations > noncostly rewards.

during the BART. Behaviorally, adolescents with greater family obligation values had lower mean pumps ($\beta$ = –.31, $p$ < .05; Telzer, Fuligni, Lieberman, & Gálvan, 2013b). In other words, adolescents who placed greater value on helping and supporting their family pumped the balloons less, an index of less risky behavior. At the neural level, family obligation values were negatively correlated with activation in the bilateral ventral striatum during cash-out trials (Figure 14.5A). Thus, adolescents with the strongest family obligation values demonstrated the lowest levels of ventral striatum activation during the acquisition of rewards.

To demonstrate that this reduced striatum sensitivity is protective, we examined how ventral striatum activation relates to health-compromising risk-taking behavior. Adolescents completed a modified version of the Adolescent Risk Taking Scale (Alexander et al., 1990), which measures the frequency of engaging in risky behavior, including stealing or shoplifting, driving in a car without wearing a seat belt, and having sex without using protection. As predicted, we found that decreased ventral striatum activation was associated with less risk-taking behavior (Figure 14.5B; Telzer et al., 2013b). These findings suggest that adolescents who value family obligation more show reduced reward sensitivity during risk taking, and this reduced reward sensitivity predicts lower rates of health-compromising risk taking in youths' daily lives.

## Family Obligation, Cognitive Control, and the Brain

We next sought to examine whether family obligation was associated with increased cognitive control. The same 48 Mexican adolescents described previously completed a standard cognitive control task, the Go/NoGo. Participants were presented with a series of rapid trials (1 s each), each displaying a single letter, and were instructed to respond with a button press as quickly as possible to all letters except for X. The X occurred in 25% of trials. Thus, participants develop a pre-potent response to press (Go) upon stimulus onset, and they must inhibit the Go response on X trials (NoGo). Response inhibition was operationalized as successful NoGo trials (i.e., overriding the pre-potent "go" response) compared to Go trials. We found that higher family obligation values were positively correlated with activation in the left dorsolateral prefrontal cortex (DLPFC), a brain region involved in cognitive control (Figure 14.6A). In other words, adolescents with the strongest family obligation values demonstrated the highest levels of DLPFC activation during behavioral inhibition. Thus, greater family obligation values may relate to a more mature use of the cognitive control system; these adolescents may be more motivated to engage in self-control.

To demonstrate that this heightened DLPFC activation is protective, we examined how DLPFC activation relates to adolescents' self-reported decision-making skills. Adolescents completed the Flinders Adolescent Decision Making Questionnaire (Mann, Harmoni, & Power, 1989), which measures decision-making vigilance (e.g., "I take a lot of care before I make my choice" and "I like to think about a decision before I make it") and decision-making avoidance (e.g., "I avoid making decisions" and "I put off making decisions"). As we predicted, higher DLPFC activation was associated with better decision-making skills (Figure 14.6B; Telzer et al., 2013b). Together, these findings suggest that family obligation may reduce risk taking by decreasing the neural imbalance during adolescence, helping adolescents to better regulate emotional decisions and impulses.

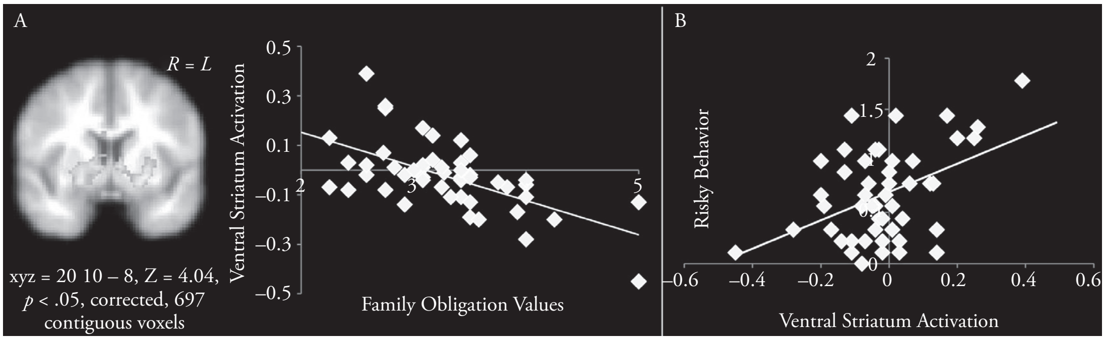

**Figure 14.5** (A) Ventral striatum activation correlated negatively with family obligation values during cash outs on the BART. (B) Lower ventral striatum activation was associated with lower levels of risk-taking behavior.

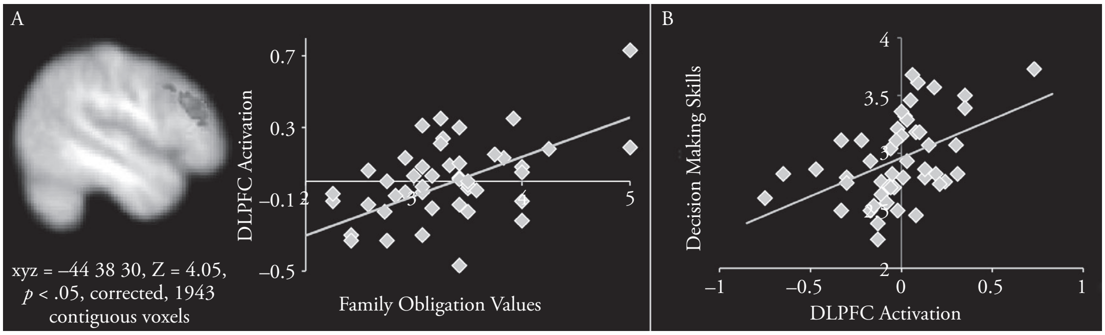

**Figure 14.6** (A) Family obligation values correlated with increased DLPFC activation during cognitive control (NoGo > Go trials). (B) Greater DLPFC activation was associated with better self-reported decision-making skills.

## Family Obligation as a Unique Cultural Resource

Next, we examined whether adolescents' reports of family cohesion show similar patterns as those found for family obligation values. We ran the same analyses as those described previously, this time correlating family cohesion and support with brain activation during risk taking and cognitive control. Interestingly, family cohesion did not correlate with activation during the BART or the Go/NoGo task. Importantly, family obligation continued to predict neural activation above and beyond the effects of family cohesion. Therefore, family obligation represents a unique aspect of family relationships, suggesting that it is not necessarily about being close to one's family or feeling support from them. Rather, these findings suggest that it is more about engaging in a meaningful, culturally important family relationship that is protective and relates to reduced sensitivity to rewards and increased cognitive control.

## Do the Rewards of Family Obligation Offset the Rewards of Risk Taking?

In our final set of analyses, we sought to examine whether the rewarding and meaningful nature of family obligation offsets the rewards of risky behavior. We correlated ventral striatum activation during the family assistance task with ventral striatum activation during the risk-taking task. As shown in Figure 14.7, adolescents who demonstrated heightened ventral striatum activation during the family task showed dampened activation in the same brain region during the risk-taking task. These findings suggest that the meaningful and rewarding nature of family obligation may make risk taking comparatively less rewarding. In addition, we correlated ventral striatum activation during the family task with DLPFC activation during the cognitive control task. Greater ventral striatum activation was associated with greater DLPFC activation, corroborating that the rewarding and meaningful nature of family obligation is associated with increased cognitive control-related neural activation.

## Putting All the Pieces Together

Previous reports have shown that increased family obligation values are associated with decreased risk taking (e.g., German et al., 2009; Gil et al., 2000; Kaplan et al., 2001; Ramirez & de la Cruz, 2003), but the neural mechanism underlying this relationship remained elusive. Placing all of our findings within our framework (Figure 14.3), we found that (1) family obligation is related to lower levels of substance use; (2) family obligation is associated with increased ventral striatum activation during a family donation task, highlighting the meaningful and rewarding nature of the activity; (3) family obligation is also associated with lower ventral striatum sensitivity during a risk-taking task and increased cognitive control-related brain function during a cognitive control task, suggesting that reward sensitivity and self-control may be altered by adolescents' motivation to avoid risk taking; (4) ventral striatum activation during the family donation task predicted lower levels of ventral striatum activation during the risk-taking task and greater DLPFC activation during the cognitive control task; and (5) all these neural activations predict lower levels of risk-taking behavior (Figure 14.8).

Together, our findings suggest that family obligation is a rewarding and meaningful family relationship that is unique from other types of close family relations (e.g., cohesion). The culturally meaningful nature of family obligation may provide adolescents with the motivation to avoid health-compromising risks. Such motivation is manifested in reduced

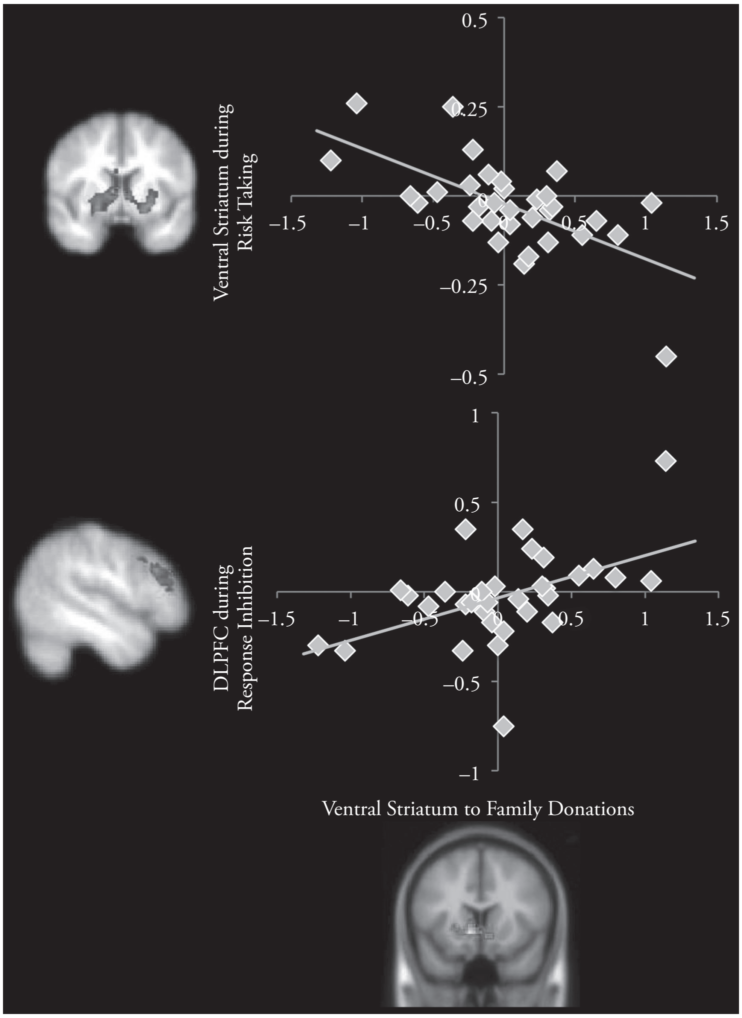

**Figure 14.7** Ventral striatum activation during the family assistance task is associated with reduced ventral striatum activation during the risk-taking task (upper plot) and increased DLPFC activation during cognitive control (lower plot).

reward sensitivity to risk taking and increased cognitive control, thereby reducing the neural imbalance that is thought to underlie adolescent risk taking. This framework and interpretation is well depicted by the following quote from a 15-year-old adolescent from a Mexican immigrant family who is talking about her family:

> Because they did a lot for me, like, they've given me this, that, and just like, I don't know. I guess just, get grades for them. Like make them proud. Um, get good grades, no drugs, no gangs, um, just being, mellow. Well not mellow, but like just staying out of trouble.

As this adolescent explains, her parents have made significant sacrifices for her. To pay them back for doing so much for her, she is actively trying to stay out of trouble. She is motivated to avoid risks for the sake of her family.

## Implications for Closing the Gap in Population Health Disparities

### *Family Obligation, Risk Taking, and Mental Health*

Results of our work have significant implications for reducing risk taking among adolescents. Our findings indicate that family obligation is a unique aspect of family relationships that reduces risk taking above and beyond the effects of more general family cohesion. Therefore, family obligation is an important type of family connection that may provide a larger sense of purpose and meaning in that adolescents have responsibilities to others. Thus, family relationships that foster self-regulatory skills and

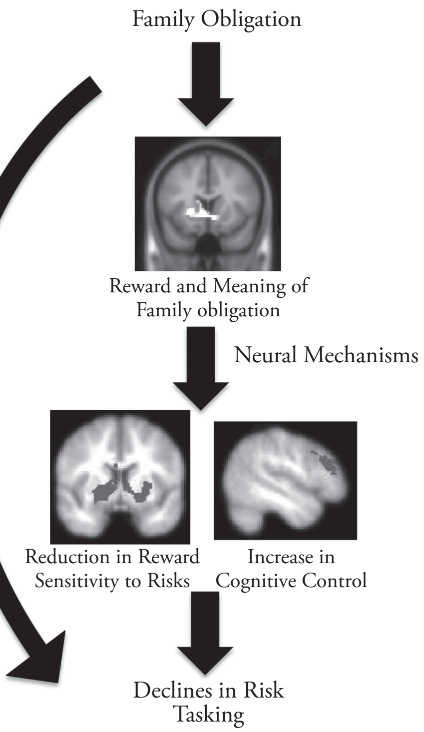

**Figure 14.8** Links between family obligation values, neural processing, and risk taking behavior.

an avoidance of behaviors that could have negative consequences may be particularly protective against adolescent risk taking. These findings suggest that interventions designed to increase family cohesion and support may not have lasting effects on adolescent risk taking. Instead, interventions should be designed to target relationships that allow adolescents to practice self-control, to put the needs of others before their own, and to increase the perception that their behaviors can impact others in negative ways.

Second, family obligation is a meaningful and rewarding activity for adolescents, and the extent of this reward is associated with reduced risk taking during the high school years. Adolescents who showed greater ventral striatum activation when providing assistance to their family showed longitudinal declines in risk taking. The meaningful nature of family obligation is perhaps the most distinctive aspect of this type of family relationship. Indeed, in our prior work, we have found that adolescents who help their family believe that they are fulfilling important roles within their family, and this relates to higher levels of happiness (Telzer & Fuligni, 2009a). Thus, the meaning attained from this activity appears to be particularly protective. These findings are consistent with work highlighting how eudaimonic well-being is adaptive and relates to long-term well-being. Eudaimonic behaviors, such as family obligation, are thought to be intrinsically meaningful, inherently good for the individual, and congruent with one's personal values, therefore leading to long-term well-being (Steger, Kashdan, & Oishi, 2008). Thus, adolescents with high levels of eudaimonic rewards may develop long-lasting psychological and social resources, leading to more resilience and better well-being. These findings suggest that interventions should direct adolescents toward meaningful activities. If adolescents engage in behaviors that are personally meaningful and rewarding, they may be less inclined to engage in risk taking.

### *The Rewards Versus Burdens of Family Obligation*

Although family obligation is a rewarding and meaningful aspect of family relationships, it is not always a protective factor. For instance, family obligation behaviors (e.g., providing support and assistance to one's family by helping around the house, taking care of siblings, and running errands) within high-conflict homes are related to heightened substance use (Telzer et al., 2014). Moreover, we have found that family obligation values are experienced as demanding (Telzer & Fuligni, 2009a), relate to declines in the academic performance of Mexican American youth (Telzer & Fuligni, 2009b), and take a toll on adolescents' physical health (Fuligni, Telzer, et al., 2009). Thus, family obligation may be stressful for some adolescents due to the burden of taking on extensive household tasks in the face of competing demands such as socializing with friends and studying for school. The stress associated with family obligation can be significant because adolescence is a developmental period during which individuals may be particularly reactive to stressors (Gunnar, Wewerka, Frenn, Long, & Griggs, 2009; Romeo, Karatsoreos, Ali, & McEwen, 2007; Romeo & McEwen, 2006). Therefore, family obligation values can be protective, but the translation of these values into actual behaviors can be burdensome. Interventionists, teachers, and clinicians should be aware of the important role that family assistance behaviors may play in adolescents' daily lives.

### *Cultural Context of Adolescent Decision-Making*

Dual-systems models of adolescent development suggest that adolescents are predisposed toward risk taking due to an imbalance between the early maturation of limbic motivational and emotional systems and a slower or later maturation of prefrontal cortical control (Casey et al., 2011; Steinberg, 2008). The dual-systems model has offered promising ways to understand the development of risk taking during adolescence, but we know little about how social processes interact with these neural processes to impact risk taking (Crone & Dahl, 2012; Pfeifer & Allen, 2012). Results from the studies presented in this chapter provide evidence of the complexity of adolescent brain–behavior relationships and provide new ways to understand neural processes underlying adolescent risk taking.

Not all adolescents engage in maladaptive, health-compromising risky behavior. Although risk taking may represent a normative developmental experience, there are significant individual differences in the severity of this risk taking. Some adolescents actively seek out thrilling experiences and engage in deviant behaviors, whereas other adolescents avoid behaviors that can have negative consequences. Some adolescents experiment with and become addicted to drugs, whereas other adolescents choose to avoid substance use. A normative, one-size-fits-all neural imbalance during adolescence cannot explain these individual differences in adolescent risk taking. The extent of the neural imbalance present during adolescence may vary across individuals depending on the cultural context of decision-making. Reward sensitivity may be high under some contexts for some adolescents (e.g., for youth high in family obligation values when engaging in family-oriented behaviors) but low during other contexts (e.g., for youth high in family obligation values when engaging in risk behavior).

Together, the results of these studies suggest that the functional maturation of brain regions involved in reward and cognitive control can be altered by cultural experiences. By engaging in meaningful family relationships that provide adolescents the opportunity to practice self-control and place their family's values and needs before their own, adolescents may show maturation in functional brain development. However, given that these data do not examine brain function across time, it is also possible that adolescents whose brains differ in meaningful ways have developed stronger family obligation values as a function of that brain maturity.

## Conclusions

Families from Latin American backgrounds represent the largest ethnic minority group in the United States, and adolescents within these families face substantial challenges to their behavioral adjustment. Results of our work indicate that traditional family values and practices play a critical role in shaping Mexican adolescents' risk for substance use and risk-taking behaviors. We examined an aspect of family life that is culturally relevant to Mexican families. By using cultural neuroscience techniques, we were able to identify a cultural resource, highlighting the underlying neural mechanisms by which family obligation is protective. Importantly, family obligation is a fundamental aspect of family life among adolescents from Mexican backgrounds, is a meaningful and rewarding behavior, and thus has important implications for risk taking and substance use. Mexican adolescents' decisions to engage in risk taking appear to depend, in part, on their cultural values.

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CHAPTER

# 15

# Cultural Differences in Emotional Expressions and Body Language

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**Abstract**

As our environment becomes increasingly more international, we are interacting increasingly more with people from different cultures. During social interactions, it is important to respond appropriately to the cues that are relevant in a given situation. People are expected to behave in a suitable way to avoid offending others. For example, an appropriate response to a greeting can avoid much misunderstanding. Cultural variations have often been named as possible factors for explaining differences in processing emotions. Because culture is in part about regulating social interaction, one expects to find that cultural norms define display rules that are at least characteristic of the daily expressions of emotions. This chapter addresses whether there are important cultural factors that determine whole-body expressions of emotion, how they are perceived, how they are displayed, and what they are.

**Key Words:** culture, neuroscience, body expressions of emotion, social interactions, processing emotions

## Cultural Perspectives on the Perception of Body Expression

With current communication technologies and global enterprises, our environment is becoming more international every day. This means that we are interacting increasingly more with people from different cultures. During social interactions, it is very important to respond appropriately to the cues that are relevant in a given situation. People are expected to behave in a suitable way in order to avoid offending others. For example, an appropriate response to a greeting can avoid a lot of misunderstanding, and correctly judging the intentions of one's business partner can make all the difference between reaching a desirable deal or not. Cultural variations have often been named as possible factors for explaining differences in processing emotions. Because culture is in part about regulating social interaction, one expects to find that cultural norms define display rules that are at least characteristic of the daily expressions of emotions. This chapter addresses the questions of whether there are also important cultural factors that determine whole body expressions of emotion, how they are perceived, how they are displayed, and what they are.

The few studies that have investigated cultural aspects of body expressions and emotion have examined facial expression recognition in different cultures. Again, the vast majority of research articles on cross-cultural differences in emotion perception have examined the recognition of facial expressions. In briefly reviewing this literature, one notes that there is nothing like a systematic analysis of the kinds of questions and the types of issues that belong specifically here. In many of the studies, it is not clear where, at what level, and at what stage during individual face processing cultural effects can enter the processing routines. The notion of *culture* is rarely commented on, and that of *race* is usually used at a descriptive level only, sidestepping the sophisticated analyses that biologists and anthropologists use nowadays to understand this term.

One might view this set of questions as belonging to the new field of cultural neuroscience, expecting that they will be treated more systematically in the near future. Growing insight in the neurological processes underlying face and emotion recognition, the influence of race and culture on these processes, and cultural variations in display rules provides a framework for the much needed research on cultural differences in the bodily expressions of emotion and social interactions.

## Culture, Race, and Face Perception

The main aspects of faces that have been studied from a cross-cultural perspective are identity, expression, and gaze direction. A fourth aspect is equally interesting and concerns cultural differences in the way observers from different racial and cultural backgrounds take advantage of multiple and parallel channels of social information input, such as recognizing a person's emotion from his facial expressions as well as from his tone of voice. We briefly review some relevant studies in each of these areas.

### *Race and Person Identity*

Face perception has been a topic of extensive research, and whether people perceive faces of their own race differently than those of other races has been of interest to researchers for over 50 years. The phenomenon known as the "other race effect" refers to the fact that people are better at recognizing faces from their own race than faces from other racial groups (Lindsay, Jack, & Christian, 1991; O'Toole, Deffenbacher, Valentin, & Abdi, 1994; for review, see Meissner & Brigham, 2001). Our lab performed a few experiments on the other-race effect using Chinese subjects who had no previous exposure to Caucasian faces. We used an extensive battery of tasks that were available from previous experiments in our laboratory. The tasks had been developed to investigate both neurologically intact and impaired observers, as well as various clinical populations. Therefore, these tasks taxed verbal and cognitive functions (e.g., memory) as little as possible. For example, during all match-to-sample tasks, one picture was always presented on top, and a matching picture had to be chosen from the two pictures below. One experiment focused on identity recognition and required matching the target stimulus shown in frontal view to the correct foil shown in three-fourths profile. One block presented Caucasian faces and the other Chinese. We did not find the other-race effect since our results showed no difference between groups or stimuli (Sinke, 2012).

One important and well-studied phenomenon in face recognition pertains to the idea that recognition of the face is more dependent on holistic, or configural, processing than, for example, object recognition (Tanaka & Farah, 1993). Consequently, it has been surmised that the other-race effect could be explained by improved holistic processing for same-race faces (Michel, Rossion, Han, Chung, & Caldara, 2006). In our lab, we recently created the identity face-matching task as described previously with South African faces from a Xhosa population. Caucasian students performed the task with upright and inverted Caucasian and South African faces. In line with the other-race effect, Caucasian participants showed higher accuracy rates and faster reaction times on Caucasian than on South African faces. This task also allows the creation of a measure of configuration processing as measured with the face-inversion effect (Farah, Tanaka, & Drain, 1995; Yin, 1969). Interestingly, the inversion effect was comparable for both Caucasian and South African faces, so the other-race effect as found in this study could not readily be explained by an effect of race on configural processing. These results are in line with those of other studies that found evidence for the other-race effect even though no differences in configural processing could be found, giving rise to the idea that the other-race effect cannot be completely explained by differences in holistic processing (Michel, Caldara, & Rossion, 2006; Mondloch et al., 2010). In addition, these effects have been studied using an event-related potential (ERP) known to be specifically involved in face processing, the N170 (Eimer, 1998). The studies investigating the face inversion effect show slightly different but, again, somewhat varied results, indicating that both same- and other-race faces are processed holistically, although it may be delayed for other races (Wiese, Stahl, & Schweinberger, 2009) or increased for same-race faces (Caharel et al., 2011; Gajewski, Schlegel, & Stoerig, 2008; Montalan et al., 2013; Vizioli, Foreman, Rousselet, & Caldara, 2009). In contrast, Hahn, Jantzen, and Symons (2012) found that same-race faces were processed more holistically than faces from other races using a technique called "Thatcherization," rotating only the eyes and mouth within a face.

Another important aspect in cross-racial facial recognition is the extent to which people have experience with other races (Bukach, Cottle, Ubiwa, & Miller, 2012; Rhodes et al., 2009; Stahl, Wiese, & Schweinberger, 2008). In addition to the race of the perceived person, and the degree to which perceivers have experience with other races, Michel, Corneille, and Rossion (2010) showed that the degree to which the same, racially ambiguous face is processed holistically depends on what the observer perceived to be the race of the stimulus. Another explanation for racial differences in holistic processing may be baseline differences between people of different races. For example, there is evidence that Asians may process faces and other stimuli more configurally than Caucasians (Michel, Caldara, et al., 2006; Tanaka, Kiefer, & Bukach, 2004, for an overview, see Miyamoto, 2013). Our lab recently conducted a part-to-whole matching experiment in Japan. Participants matched eyes or mouths to a picture of a whole Caucasian face, or they matched doors or windows to a picture of a whole house. Accuracy scores and reaction times of the Japanese participants were similar to those of a Dutch control group and, furthermore, they showed the same pattern in face and object part recognition as a Dutch control sample. In short, the Japanese participants did not show an other-race effect, which may be explained by these baseline differences in holistic processing between populations.

The next question concerns the time during perceptual processing when race influences face perception. Walker and Tanaka (2003) found this race effect already at early stages of perceptual encoding by using a sequential matching task with natural and morphed East Asian and Caucasian faces. However, the N170 ERP has given rise to larger amplitudes for other than same race faces (Caharel et al., 2011; Gajewski et al., 2008; Herrmann et al., 2007; Stahl et al., 2008; Walker, Silvert, Hewstone, & Nobre, 2008). This was not seen in the earlier P100 ERP (Caharel et al., 2011; Herrmann et al., 2007; Stahl et al., 2008). Thus, a race effect seems to manifest itself at a later stage, related to the structural encoding stage of the face and later, at approximately 250–300 ms (Caldara, Rossion, Bovet, & Hauert, 2004; Caldara et al., 2003; Tanaka & Pierce, 2009). In conclusion, the picture of the other-race effect is still not very solid and the explanation is not clear, as one can also discern from recent meta-analysis reports (Michel, Rossion, et al., 2006; Young, Hugenberg, Bernstein, & Sacco, 2012).

### *Race and Facial Expressions*

Facial expressions play a major role in communication, but this role may be modulated by culture or race. The debate on universal facial expressions of basic emotions has been occurring for decades (see Nelson & Russell, 2013; Scherer, Clark-Polner, & Mortillaro, 2011). Currently, however, many researchers take a position that is a sort of compromise between the classical Ekman position on universal emotions enshrined in the Ekman facial expressions and the realization that there is a measure of cultural relativity.

A modest position that only touches that debate tangentially concerns the influence of culture at the level of the display rules for emotions. Culture provides various kinds of rules about which facial expressions to display, when, and where. This is a vast topic, and dealing with it systematically would require contributions from anthropologists and sociologists, among others. To illustrate, there is cultural variability in the level of the display rules for emotions. For example, Japanese people are perceived as less likely to show negative emotions such as fear or anger but more likely to express positive emotions (Hess, Blairy, & Kleck, 2000). At the least, there are cultural differences in the appropriateness of expressing certain emotions in certain situations. Overall, Asians are less prone to express negative emotions such as contempt and fear (Chung, 2012; Safdar et al., 2009). A well-known experiment showed that Japanese participants were prone to mask negative emotions by smiling, whereas Americans did not (Friesen, 1972). Evidence for this emotion suppression was found when Asian and American participants were asked to suppress their emotion in response to images while ERPs were recorded. In Asian participants, but not in Americans, a significant decrease in the late positive potential (LPP), a measure of emotional processing, was found (Murata, Moser, & Kitayama, 2013). Possibly because of these traditions, people in some East Asian countries tend to be more emotionally introverted (Bond, 1993; Matsumoto, Yoo, Hirayama, & Petrova, 2005).

Because of these cultural differences in display rules, it can be hypothesized that Asians are more experienced than Westerners in estimating emotional states from looking at the eyes because it is well-known that muscles around the eyes (orbicularis oculi) are difficult to control (Ekman & Friesen, 2003). An interesting day-to-day result of this focus on the eyes can be seen in emoticons used in different areas of the world (Pollack, 1996). Whereas Westerners keep the eyes constant (two simple dots) but change the mouth to signify different emotions, Japanese keep the mouth as a straight line while changing the eye symbols for each emotion. To test this cultural bias on the eye versus the mouth, Yuki, Maddux, and Masuda (2007) used both emoticons and real faces and manipulated independently the eyes and mouths. They found that Japanese participants rated the emotion by focusing mainly on the eyes, whereas American participants used the mouth as a prominent cue (also see Blais, Jack, Scheepers, Fiset, & Caldara, 2008). These findings are supported by a study that examined the eye movements of Eastern and Western participants during the decoding of facial expressions. It was found that Eastern people, in contrast to Westerners, fixate on the eye region instead of looking at multiple regions of the face. In addition, these different scan patterns are likely to be an underlying cause of recognition deficits in certain emotions (Jack, Blais, Scheepers, Schyns, & Caldara, 2009). In contrast, Asians and Caucasians were found to use largely the same cortical networks while trying to decode emotion from the eyes of both their in-group and their out-group, although these networks were more active in response to eyes belonging to the same race (Adams, Rule, et al., 2010).

Also on a more physical level, emotions are not always expressed similarly or to the same degree between different cultures (Elfenbein, 2013). For example, when participants from Quebec and Gabon were asked to freely express emotions, it was found that the groups used different action units for different emotional expressions (Elfenbein, Beaupre, Levesque, & Hess, 2007). In other words, people from different cultures use different facial muscles to express emotion. It may therefore not come as a surprise that what people expect to see in an emotional expression differs as well. This cultural variety was demonstrated by adding random noise to a standard face or by using a random action unit generator to create random expressions, after which participants were asked to judge the emotion seen in the random noise. These responses were then used to create average expected emotional expressions, which differed in each culture (Jack, Caldara, & Schyns, 2012; Jack, Garrod, Yu, Caldara, & Schyns, 2012). Also, there is evidence supporting the notion that the left side of the face may be more strongly influenced by culture than the right side and that there are cultural differences in these hemifacial biases (Elfenbein, Mandal, Ambady, Harizuka, & Kumar, 2004; Mandal, Harizuka, Bhushan, & Mishra, 2001). These effects are important to take into consideration not only for researchers who are interested in facial responses, emotional contagion, or imitation but also because they may be of importance for new emerging techniques such as facial interpretation software for smartphones, security cameras, or games. In conclusion, it seems that a Facial Action Coding System (FACS; Ekman & Friesen, 1978), which maps all the muscles used for facial expressions, would need to be different for each culture.

Probably because of these differences in the expression of emotion, there are subtle differences in how people from different countries interpret facial expressions of emotions (Elfenbein & Ambady, 2002). There seems to be an in-group advantage especially for the recognition of culturally "natural" emotions and a majority advantage for standardized (FACS) expressions (Beaupre & Hess, 2005; Elfenbein et al., 2007; for review, see Kang & Lau, 2013). In a functional magnetic resonance imaging (fMRI) experiment, Chiao et al. (2008) showed Japanese and American participants emotional faces of their in- and out-groups, and it was found that the amygdala responded more strongly to fearful expressions of the in-group. However, there may also be differences in the way the Japanese brain and the Caucasian brain process emotion to begin with; it was found that the Japanese rely more on the premotor cortex and the insula, whereas Caucasians recruited the posterior cingulate, the supplementary motor area, and the amygdala (Moriguchi et al., 2005).

A meta-analysis by Elfenbein and Ambady (2002; see also Elfenbein & Ambady, 2003) clearly showed that the in-group advantage was reduced when more intercultural contact was established. An fMRI study found that culture and duration of stay influenced amygdala activation and its relationship to the recognition of anger and disgust (Derntl et al., 2009). Studies of cultural factors need to more systematically compare results obtained with groups before and after they have had extensive exposure to the other culture. In any case, living in a multicultural environment or not must be a relevant factor. Therefore, in our experiment, we tested Chinese students who had recently arrived in The Netherlands (no more than 2 weeks) so that their contact with Western people was at a minimum. The previously mentioned study on Chinese versus Dutch identity recognition also contained a memory experiment. Dutch and Chinese participants were asked to memorize a set of Caucasian faces. In one experiment, the faces wore neutral expressions. The Dutch participants performed significantly better than the Chinese. However, the difference between the two groups disappeared when the faces to remember were showing a fearful, sad, or happy expression. This suggests that neutral faces of strangers are more difficult to remember. It also indicates that memory for faces of people from another race is at least to some extend culturally specific, but it may also be dependent on emotion and probably the interplay between race and gender (Krumhuber & Manstead, 2011). However, the pattern was different when we used a task that required matching an expression to the correct similar one rather than a memory test. Overall, the Dutch participants were rather faster than Chinese participants in matching the Caucasian facial expression. However, this was also dependent on the emotion; Chinese students were slower than the Dutch on all emotions except *happy. Fear* and *surprise* were recognized less accurately in the two groups than the other emotions. Taking these and previous results into consideration, *happy* seems to be the facial emotion most easily recognized across cultures.

### *Culture and Gaze*

Humans use information on the direction of gaze of others to rapidly orient themselves to the location where the gaze is directed—a process that is useful to detect relevant events in the environment. However, this automatic orienting behavior seems to be influenced by the in-group versus out-group status of the observed face. For example, an Italian study showed that black participants shifted attention similarly to the averted gaze of black and white faces, whereas white participants selectively shifted attention only in response to individuals of their same group (Pavan, Dalmaso, Galfano, & Castelli, 2011). Another study showed that the own-race effect for the memory of faces is also dependent on eye gaze, where same-race faces were recognized better only when the gaze was direct (Adams, Pauker, & Weisbuch, 2010). It is interesting to note how some effects that were previously deemed to be automatic attention effects are now found to be under the control of social factors (Shepherd, 2010). Certainly, more research is needed to unravel the various components of these complex behaviors, and it might also shed light on the question of cultural or racial influences on the perception of bodily expressions. Comparable to gaze direction, body language provides directional information, and a disruption of these processes as a result of racial interactions can be indicative of the effect of race on body language.

Regarding the perception of emotion and gaze, it was found that East Asians experience a face as angrier when the eye contact is direct (Akechi et al., 2013). Furthermore, another study found that the direct gaze of out-group members is experienced as more intense than the gaze of in-group members in an Asian versus Caucasian comparison (Kramer et al., 2013). This may be explained by greater amygdala responses to the direct gaze of out-group members (Adams, Franklin, et al., 2010; Richeson, Todd, Trawalter, & Baird, 2008).

## Culture and Affective Cue Selection

To date, cross-cultural studies of emotion have typically used facial expressions not accompanied by information from the voice as expected in the natural environment (de Gelder & Bertelson, 2003; de Gelder, Bocker, Tuomainen, Hensen, & Vroomen, 1999; de Gelder & Vroomen, 2000; Massaro & Egan, 1996). However, there are indications of cross-cultural differences in the way information from the face and information from the voice are combined. Cultural differences were reported not only in unisensory stimuli but also in the susceptibility to ignore information in visual (Masuda et al., 2008) and auditory (Ishii, Reyes, & Kitayama, 2003) modalities. The very process of integrating emotional cues from different modalities may also be culture sensitive. We investigated cultural differences in the multisensory perception of emotion between Japanese and Dutch participants. In line with the view that the Japanese are sensitive to contextual information (Masuda et al., 2008) and to vocal affect (Ishii et al., 2003), we expected that they would weigh cues in the voice more than the Dutch when presented with audiovisual stimuli. We used short fragments voiced by two Japanese and two Dutch female speakers in their native language. Each fragment with neutral linguistic meaning was uttered with happy or angry emotion, and the fragments were combined with happy and angry facial expressions. Our results demonstrated that when the face and the voice did not represent the same emotion, the Japanese participants weighted cues in the voices more than did the Dutch participants. These findings provide the first evidence that culture modulates multisensory integration of affective information (Tanaka et al., 2010). The results are consistent with those of a study reporting that the Japanese are more susceptible to affective prosody and less susceptible to linguistic content compared to Americans (Ishii et al., 2003). Our results are also consistent with a lesser degree of audiovisual speech integration in the Japanese (Sekiyama & Tohkura, 1991). These results can be interpreted as showing that in multisensory situations, the Japanese people rely more on a vocal affect than a facial expression because direct or excessive eye contact can be considered rude in their culture (Malpass & Kravitz, 1969) or because they tend to use a less efficient strategy to judge the facial expression (Jack et al., 2009). It also may be related to the fact that Japanese people control the display of their own feelings in the face (Ekman, 1972; Matsumoto, Takeuchi, Andayani, Kouznetsova, & Krupp, 1998). This may lead to a lower reliance on the face and higher reliance on the voice when judging a person's emotion.

### Cultural Differences in the Recognition of Bodily Expressions

Although there is no doubt that the face, or voice, can indicate much about a person's feelings or intentions, body language is another very important indicator. Bodily expressions of emotion have only recently become a domain of interest, and knowledge in this area is increasing rapidly (for reviews, see de Gelder, 2006; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; de Gelder et al., 2010), although cultural differences in perceiving bodily expressions have not yet received much attention. We previously stated that facial expressions can be culturally diverse, and there is evidence that the same might be true for bodily expressions. In 1988, Scherer et al. found that the Japanese do not use as many movements of the hands, arms, and body in certain emotional situations. Furthermore, the Japanese and Americans have some unique and differing features that enable them to recognize emotion from body posture, whereas other features may be universal. For example, a bent head and arms hanging next to the body are essential for Japanese participants to recognize sadness, but Sri Lankans and Americans accept other poses for sadness as well. Also, poses that are viewed as fearful by Japanese people are perceived as angry by Sri Lankans (Kleinsmith, De Silva, & Bianchi-Berthouze, 2006; Sogon & Masutani, 1989). The study by Kleinsmith et al. (2006) also supports the theory that some cultures may be less expressive: When American and Japanese participants are asked to rate how intensive the emotion is that a person must be feeling based on bodily expression, the ratings of the Japanese are higher than those of Americans. The same was previously found for Chinese participants: The Chinese rate facial expression of negative emotions of other Chinese as more intense than those of Caucasians (Zhu, Ho, & Bonanno, 2013). This implies that a Japanese observer infers that someone might be feeling more than she is expressing. On the other hand, although cultural diversity exists, it seems that there is at least some universality with regard to recognizing emotional expressions in the body. For example, Americans and Indians were asked to categorize emotional dance expressions as described in ancient Indian texts, and both groups were able to do this accurately (Hejmadi, Davidson, & Rozin, 2000). Similarly, in-group and out-group effects, as discussed with facial expressions, may be similar with regard to bodily expressions: Caucasians are faster to recognize angry body language when a black face is combined with an angry body than when a Caucasian face is combined with the exact same angry body (Hinzman & Kelly, 2013). In contrast, African and American children judged the expression of emotional faces, faces and bodies, and bodies alone, and no cultural differences were found in the body-only condition (Tuminello & Davidson, 2011).

Additionally, in a recent behavioural study, we found that white Western European participants perceived black bodies of ambiguous emotion as angrier than ambiguous white bodies when in a neutral context (i.e., paired with neutral sounds); however, when the bodies were paired with affective sounds there was no difference in emotion categorization, suggesting that specific multisensory contexts may be able to reduce or eliminate race-specific biases in emotion perception. We also investigated the cerebral correlates of "other race" body emotion perception, scanning white European participants using fMRI. Here, we clearly saw regions which activated more to other race, vs. own race bodies, including the bilateral interparietal lobule and fusiform gyrus.

In our lab, we tested the same group of Chinese subjects with instrumental and emotional bodily expressions, and the procedure was the same as that used for faces. Here also, no differences were found between groups or stimulus categories. In contrast with the facial expression results, where *happy* is the best recognized expression, *sad* seems to be the most prominently recognized body emotion for both groups. In a follow-up experiment using images of day-to-day scenes with and without other people present, we investigated the role of the context in which bodily expressions are encountered. When judging the emotion of bodily expressions shown in nonsocial contexts, we found that the Chinese were generally slower in judging the emotion of the target body than the Dutch. However, because we had also found this for the previous match-to-sample tasks in general, we cannot say conclusively that it is because of the context. Both groups were distracted by a fearful context when the body is neutral, leading to more time taken to respond.

In addition, bodily expressions in social contexts that show other people engaging in activity with either the same or a contrasting emotional significance are more difficult to recognize by either group when the bodily expression is incongruent with the scene. All participants were influenced by an incongruent (happy or neutral) social scene showing fearful target bodies and also by a fearful social scene showing happy target bodies (as shown by the accuracy data). However, the Chinese did perform better than the Dutch students in general, which was not the case when the bodies were presented in a nonsocial context or without context. An explanation for this could be that the Chinese are in fact more influenced by the social scene, but in a different way: Because there are other people present in the scenes, they might feel some pressure to perform better. We know that such unrealistic social cues can indeed have an influence on behavior (e.g., Bateson, Nettle, & Roberts, 2006), and because the Chinese students were raised in a collectivistic society, this could have a greater effect on them. One possible explanation of why the incongruent social scenes do not distract could be the short stimulus duration of 100 ms. A previous study showed that Japanese participants who had to judge a target body within a social scene looked more at the other people in the scene—but only after 1 s (Masuda et al., 2008). This finding, however, could not be attributed to any ambiguity in the scenes: Both groups recognized the emotion expressed by the people in the scene equally well, and neither had any trouble recognizing happy scenes.

In addition, Chinese participants seemed to be more specialized for faces compared to Dutch participants; they were more accurate in recognizing both Chinese and Caucasian identities, and they did this faster than identifying shoes or bodies. With regard to Caucasian emotions, Chinese participants needed more time than their Dutch counterparts independent of whether these emotions were expressed in the face or the body. They also needed more time to recognize (emotional) bodies in a nonsocial context—but not when bodies were perceived in a social context, in which case the Chinese were faster than the Dutch. Thus, although an incongruent scene similarly influenced both groups, a social scene did have more effect on the Chinese participants. One might speculate that this is related to the fact that traditional Chinese society is less individualistic than Western society. Currently, however, these are rather broad and vague categorizations.

To add to the existing literature, a bodily expression recognition experiment was performed in Japan and The Netherlands. Participants performed a sample-to-match task with angry, fearful, happy, and neutral expressions of Japanese and Dutch bodily expressions. Caucasian expressions were recognized more accurately than Japanese stimuli by both Dutch and Japanese participants. Interestingly, Japanese participants were better at recognizing fearful Japanese expressions than were the Dutch participants. However, it is important to note that Japanese angry and fearful bodily expressions yielded lower accuracy scores than those of Japanese happy and neutral expressions from both nationalities. This has previously been found for Japanese facial expressions (Malpass & Kravitz, 1969). It can be argued that these stimuli may be less expressive than the Caucasian expressions because it is culturally less accepted to express negative emotions in Japan. Further analyses on behavioral ratings of the stimuli should be taken into account.

## Cultural Differences in Social Interactions

Much research has focused on the one-sided action of perceiving the face, or body, of another human. How does race influence the process of daily interaction? Participants of four different nationalities (Irish, Guatemalan, Peruvian, and Serbian) were asked to rate the intensity of social interactions between two English people. In this situation, an in-group effect was found; Irish participants rated the emotions as more intense than did people from other nationalities (Sneddon, McKeown, McRorie, & Vukicevic, 2011). Recalling the discussion of display rules, it has been found that Asians react less angrily than Americans in an anger-provoking situation with an experimenter (Mauss, Butler, Roberts, & Chu, 2010), but they experience greater physiological responses in confrontational or intercultural social interactions (Butler, Lee, & Gross, 2009; Mauss & Butler, 2010).

Another important aspect of social interaction is the ability to understand other people not only by reading facial and bodily expressions but also by reading their gestures. Molnar-Szakacs, Wu, Robles, and Iacoboni (2007) measured corticospinal excitability—a measure of motor resonance or, in other words, the responsiveness of the motor cortex—in response to actors of the in- and out-group playing out both culturally known and unknown gestures. Interestingly, motor resonance was increased only in response to in-group members, independent of the gestures. However, another study indicated that in females, the opposite pattern can occur (Desy & Theoret, 2007). In line with these results, observing both the familiar and the unfamiliar gestures of in-group members also facilitates the mirror neuron networks and the insula (Liew, Han, & Aziz-Zadeh, 2011). In addition, cortical networks involved in imitation, including the motor areas (Losin, Iacoboni, Martin, Cross, & Dapretto, 2012), respond differently to gestures performed by people of another race.

## Conclusion

Social interactions are a large part of daily human life, and in these interactions we use information from facial expressions, body posture, and tone of voice. Race and culture are increasingly important aspects in this regard, and they influence these processes that are at the heart of successful communication. In the literature reviewed, we found that navigating in an environment with many people of other nationalities might influence one's ability to remember their faces, interpret their emotions and gestures, or even misunderstand their gaze. There are many situations in daily life in which this can have detrimental effects. For example, in doctor–patient relationships, it has been found that race may interrupt effective doctor–patient communication or impede the trust that patients have in their doctor due to misinterpretations of nonverbal behavior (Levine & Ambady, 2013). Furthermore, people were willing to listen more often to a computer avatar giving them advice when the avatar was a member of their in-group (Pratt, Hauser, Ugray, & Patterson, 2007), which can severely impact adherence to medication or treatment in a medical setting. It is reasonable to assume that this may also play a role in other real-life interactions—for example, between teachers and students, doctors and patients, therapists and clients, and police officers and the public. If these kinds of processes, essential for communication, are influenced by race or culture, the same might be true for the perception of body language in day-to-day interaction. To make the comparison with daily life, this might influence the effectiveness of police officers or firefighters working in a multicultural environment, requiring astute responses from others in a high-stress situation.

Studies on display rules have consistently found that some cultures are more likely to suppress their emotions, especially negative ones, in social interactions. This again is something that should be taken into account in important interracial interactions. For example, to take a therapist–client perspective, the role of depression on emotional expression is vastly different for people from different cultures (Chentsova-Dutton, Tsai, & Gotlib, 2010; Su, Lee, & Oishi, 2013). On a more positive note, it has been suggested that detrimental effects of emotion suppression are also dependent on culture, where the negative effects are less for people with Asian values who are more likely to suppress their emotion (Butler, Lee, & Gross, 2007).

More diverse studies with different populations are necessary. For example, fMRI studies are predominantly done on Caucasian populations, even though people from other races may have a slightly different brain structure (Bai et al., 2012; Isamah et al., 2010). Some studies have examined the previously reviewed race effects in clinical populations, such as those with autism (Hirschfeld, Bartmess, White, & Frith, 2007) or schizophrenia (Pinkham et al., 2008), finding that these syndromes do not interact with racial biases. However, it was found that children with Williams syndrome do not have racial stereotypes (Santos, Meyer-Lindenberg, & Deruelle, 2010) and that emotion perception may be differentially affected in different populations with schizophrenia (Brekke, Nakagami, Kee, & Green, 2005; Leppanen et al., 2006).

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# PART 5

# Cultural Neuroscience of Intergroup Processes

CHAPTER

16

# How Next-Generation Neuroscience Technologies Can Facilitate Comparison Across Cultural Contexts and Species: Implications for Global Health

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## Abstract

Studies in small-scale societies and nonhuman primates demonstrate evidence of xenophobia and xenophilia as basic responses to strangers. These studies highlight a cultural universal among social animals during interpersonal interaction: Group distinctions matter. We review the literature of small-scale societies and nonhuman primates, comparing them to the human social psychological literature on minimalist intergroup behavior in an attempt to delineate cognition, affect, and behavior common to intergroup contexts. In the process, we redefine culture, making it amenable to specific social groups and social contexts. We discuss the limitations of these comparisons—specifically, highly variable technological approaches, experimental environments, and paradigms. We then look forward to next-generation neuroscience technologies currently being developed that could facilitate comparison across human cultural context and cross-species in ecologically valid, unconstrained, nonlaboratory environments. We conclude by discussing the implications of these technologies for cultural neuroscience and global health.

**Key Words:** cultural neuroscience, global health, technological paradigms, intergroup processes, nonhuman primates

Cultural neuroscience holds the promise of addressing universals about the brain and behavior. By exploring common behaviors and neural mechanisms across the human species, scientists will be able to posit theories that describe how people's biology facilitates behavior, and they will be able to predict what people are likely to do on average. However, this approach is flawed unless it takes into account *all* human beings, not just formally educated people in Western, industrialized, democratic societies. Ignoring certain human beings restricts the range of social behavior attributed to culture. Moreover, this approach is flawed if it ignores species that hold large genetic similarity to human beings, such as great apes, and species that co-reside and interact with human beings, such as canines. Integrating knowledge from research on these species lets us know what aspects of culture are uniquely human or simply held over from a common ancestor.

Perhaps one reason why these flaws continue to exist is the lack of a common metric to study other species and human beings that reside in other areas of the world. Using existing neuroscience technologies on humans across the world proves problematic because they are expensive and nonportable, resulting in few sites where researchers can collect brain imaging and other neuroscience data. Existing neuroscience technologies are usually not as compatible with other species because these participants tend not to follow instructions delivered with language, and these technologies are optimized for human beings. Here, we propose a common solution to both of these problems: a hypothetical next-generation neuroscience technology that is portable, cheap, and optimized to record peripheral and central nervous system activity in human beings as well as other species.

The reader may wonder how the issue of intergroup relations is linked to questions in cultural neuroscience and global/population health. Indeed, we posit as the central theme to our chapter a commonality across human cultures and nonhuman primate species; group distinctions matter. This is at the heart of intergroup relations. When considering this phenomenon, it suggests a definition of culture that views social groups as cultural units, theaters for pro- and antisocial behavior. Because antisocial behavior such as intergroup violence is responsible for poor global and population health outcomes, understanding the commonalities of intergroup phenomena is important for consideration of cultural neuroscience and population health.

Before we describe what hypothetical next-generation neuroscience technology may be like, we review literatures in evolutionary anthropology on nonhuman primate intergroup behavior, human behavioral ecology on intergroup behavior in small-scale societies, and social psychology on minimalist groups. We describe why group distinctions matter for social behavior, before delineating the common cognition, affect, and behavior across these comparisons. We then posit a re-definition of culture, explore limitations to current neuroscience technologies and approaches, and discuss issues surrounding ecological validity. We conclude by describing next-generation neuroscience technologies and their implications for global health.

## Intergroup Relationships in Nonhuman Primates

Living in groups has costs and benefits. The primary cost of sociality is competition over resources, but the prevalence of social primates suggests that this cost is somehow balanced by the benefits of sociality (Silk, 2007). First, living in groups dilutes the per capita chance of being captured by predators (Janson & Goldsmith, 1995; van Schaik, 1983). The second benefit of sociality is cooperation, which in turn allows collaborative foraging (Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012), coalitionary defense of resources (Wrangham, 1980), cooperative breeding (Kokko, Johnstone, & Clutton-Brock, 2001), and commodity trading (Noë & Hammerstein, 1994). If we consider the formation of a group as a trade-off between resource competition and social benefits, in most circumstances individuals from out-groups do not provide any benefits; they simply intensify the competition over resources. The default response to out-group individuals is thus negative; groups compete against each other and form intergroup dominance relationships that grant the dominant group (usually the larger group) priorities to access resources (Crofoot & Wrangham, 2010). As a result, intergroup encounters in troop-living primates are mostly agonistic, which include avoidance, calling contest, display (e.g., branch dragging), and physical aggression (e.g., chasing and biting) (Cheney, 1987; Crofoot & Wrangham, 2010; Fashing, 2001; see also experimental works on rhesus macaques by Mahajan et al. (2011) and on capuchin monkeys by Crofoot & Gilby (2012)).

This competitive intergroup relationship has gone to an extreme in chimpanzees, one of our closest living relatives. Male chimpanzees not only team up to patrol borders but also form troops to raid their neighbors' territories (Boesch et al., 2008; Muller & Mitani, 2005; Wilson & Wrangham, 2003). Female chimpanzees sometimes also participate in intergroup aggression (Boesch et al., 2008) and can even become the dominant aggressors toward immigrants (Pusey et al., 2008; Townsend, Slocombe, Emery Thompson, & Zuberbühler, 2007). This xenophobic aggression is one of the leading causes of mortality in adult chimpanzees (Williams et al., 2008), reducing the numerical advantage of out-groups (Wrangham, 1999) and eventually resulting in territory expansion (Mitani, Watts, & Amsler, 2010).

Experimental work on chimpanzees is consistent with the previous mentioned observation. Chimpanzees show avoidance and defensive behaviors when they hear the call of a strange chimpanzee played by a hidden speaker (Herbinger et al., Papworth, Boesch, & Zuberbühler, 2009; Wilson, Hauser, & Wrangham, 2001). Furthermore, they adjust xenophobic responses based on the assessment of their numerical advantage over the stranger: They approach the stranger only when they outnumber him by a factor of three (Wilson et al., 2001).

Contagious yawning, or the occurrence of yawning behavior after observing others' yawns, has recently emerged as another promising paradigm to study intergroup relationships. Several experiments suggest that the contagiousness of yawns indicates the strength of social bonds: The closer the social bond between the yawner and the observer, the more contagious the yawns (gelada baboons: Palagi, Leone, Mancini, & Ferrari, 2009; bonobos: Demuru & Palagi, 2012; humans: Norscia & Palagi, 2011). Campbell and de Waal (2011) tested adult chimpanzees with yawning videos of in-group and out-group individuals and found that contagious yawning only occurred in the in-group condition.

The previously mentioned evidence suggests that nonhuman primates generally express xenophobia given the competitive relationship between groups. However, intergroup interactions could sometimes become peaceful and even prosocial (Cheney, 1987). For example, feeding competition is relaxed in gelada and Guinea baboons that feed on highly abundant and indefensible diets (e.g., leaves). They do not show agonistic responses when they hear the vocalization of strangers (Bergman, 2010; Maciej, Patzelt, Ndao, Hammerschmidt, & Fischer, 2013). Furthermore, it is possible for prosocial behavior toward strangers to evolve if the strangers bring special social benefits. In chimpanzees, immigrants are young, sexually receptive females and they, as desirable mating partners, quickly receive protection from residential males (Kahlenberg, Thompson, Muller, & Wrangham, 2008). Moreover, two groups of bonobos, the other closest living relative of our species, can engage in affiliative behaviors such as grooming, joint travel, cofeeding, and sex (Furuichi, 2011). They even voluntarily share monopolizable food with strangers (Tan & Hare, 2013). Bonobos live south of the Congo River, a habitat that is believed to be rich in food availability—that is, bonobos have experienced relaxed feeding competition (Furuichi, 2009; Hare, Wobber, & Wrangham, 2012); meanwhile, they form strong bonds with female residents, all of which have immigrated from out-groups (i.e., strangers can become future allies; Surbeck & Hohmann, 2013).

In summary, intergroup behavior in nonhuman primates is a trade-off between the costs of resource competition and the benefits of sociality. Xenophobia is prevalent in most primates because the costs usually outweigh the benefits. However, peaceful and even prosocial relationships between groups are possible if resource competition is reduced and/or the social benefits are high. This review suggests that intergroup violence (and perhaps peace) predates the origin of human cultures. Human group mindedness is likely a derivative from the primate-like intergroup behaviors and cognition.

In the next two sections, we review the intergroup relationships in two contexts: human small-scale societies and minimalist groups. We believe that these two contexts represent the robustness of human group mindedness. Small-scale societies represent the true diversity of human societies, and the prevalence of group mindedness in these societies suggests that it is a universal phenomenon. Minimalist groups represent probably the most artificial and subtle kind of groups, but humans spontaneously show in-group–out-group biases in these contexts. This suggests that group mindedness is a highly automatic process and, again, a human universal.

## Intergroup Relationships in Human Small-Scale Societies

Here, we consider human small-scale societies in which intergroup conflicts are not regulated and escalated by institutional leadership (Wrangham & Glowacki, 2012). Although highly diverse and not completely free from the impacts of agriculture and industrialization, understanding human intergroup relationships in human small-scale societies is necessary because industrialized populations are frequent outliers across various domains of human behaviors (Henrich, Heine, & Norenzayan, 2010). Like the majority of nonhuman primates (especially chimpanzees), the intergroup relationships of these small-scale societies can be highly hostile and even lethal. Intergroup violence is widespread in prehistoric and contemporary ethnic groups and is a considerable contributor to adult mortality (Bowles, 2009; Walker et al., 2013; Wrangham & Glowacki, 2012). In addition, intergroup conflicts increase during resource scarcity (Ember & Ember, 1992) and result in capture of resources (e.g., mates) (Walker et al., 2013).

The previously mentioned similarities are in support of the primate origin of human group mindedness, but intergroup relationships in small-scale societies seem to be more flexible than those of nonhuman primates. Peaceful and cooperative relationships between groups are not uncommon (Boehm, 2012; Fry & Söderberg, 2013). These intergroup alliances are linguistically negotiated and can be explained by the considerable social benefits of intergroup marriage, trade, and reciprocal sharing of resources (Chapais, 2013; Rodseth, Wrangham, Harrigan, & Smuts, 1991; Wrangham & Glowacki, 2012). Language plays a crucial role in establishing such alliances, and intergroup relationships are generally more intense between groups speaking different dialects (Aureli et al., 2008; Cohen, 2012). In corroboration, one study found that intergroup conflicts are more deadly between ethnolinguistic groups (Walker et al., 2013). This suggests that, unlike nonhuman primate groups that are only defined by geographical locations, the relationships between human groups are also mediated by other social factors such as language. These social factors might have evolved as difficult-to-fake signals of cooperative intentions that overcome the primate-like xenophobia and quickly turn intergroup competition into cooperation (i.e., tag-based cooperation; Cohen, 2012).

## Intergroup Relationships in Human Industrialized Societies

The flexible nature of human groups is more apparent in the social psychological literature, particularly the minimalist groups literature. In fact, this flexibility is often taken for granted in the literature, and much of the research on intergroup processes focuses on the mechanisms through which group categorizations occur. Although there was a surge of research on intergroup processes during the mid-twentieth century, group dynamics remain a relatively elusive topic. However, the following was been made clear: A social group can be broadly construed as two or more individuals who share a social identification and perceive themselves to be members of the same social category (Turner, 1981). The nuance of this definition is important to understand: Members of a social group do not need to share anything other than the perception that they constitute a social group. Next, we review some of the classic social psychological literature that demonstrates that in humans, group distinctions matter. Because of the enormous volume of this literature, we restrict our review to minimalist groups. A “minimal group” is created by arbitrarily placing individuals into groups (i.e., by the color of their hair) and is used to investigate the minimal conditions that are necessary to form discriminatory groups. We focus on minimalist groups to facilitate comparisons with nonhuman primates and small-scale human societies, ignoring the complex literature on racial or ethnic, age, and gender groups.

One of the most famous studies on intergroup dynamics took place at a boys’ summer camp in the late 1940s. In this study, Muzafer Sherif selected a group of 11- and 12-year-old boys to test the conditions that lead to competition or cooperation between groups. The boys, unaware of the experimental setup, were able to meet each other and interact, quickly forming groups and friendships. A few days later, the boys were arbitrarily divided into two different groups, and Sherif observed the development of these new group relations. Sherif was able to demonstrate that the two groups became competitive when they had opposing goals but worked well together when engaged in a cooperative task (Sherif, Harvey, White, Hood, & Sherif, 1961). This study was one of the first to demonstrate that intergroup hostility may arise when groups are in competition and may be allayed when the groups cooperate.

A new line of thinking emerged with the research of social psychologist Henri Tajfel. He proposed that during the process of socialization, a child categorizes social groups in terms of “we” or “they.” After the group categorizations have already been made, value judgments get associated with them (Tajfel, 1970). Although previous research had focused on similar research questions, Tajfel believed that perhaps competition was not a necessary condition to create conflict between groups. He found that the categorization alone of individuals into arbitrary social groups can elicit in-group favoritism, and he showed that when given rewards, people attempt to maximize the payoff to their group (the in-group) compared to the out-group (Tajfel, Billig, Bundy, & Flament, 1971). This research demonstrates that this *in-group favoritism* occurred when social categories were randomly established without reference to any interpersonal similarity (Billig & Tajfel, 1973). Therefore, categorization itself could be both a sufficient and necessary condition for intergroup behavior.

Studies have also found that there are many forms of in-group favoritism. For example, individuals divided into groups of two, three, or four and asked to write a solution to an organizational problem before individually rating the solutions of the other groups consistently evaluate their own group’s solution as the best (Blake & Mouton, 1962). In an attempt to isolate the minimal conditions that were sufficient to generate these types of discriminatory in-group versus out-group attitudes, categorization of individuals into arbitrary social categories elicits in-group favoritism, and the anticipation of future interactions determines the bias in individuals; whereas having the experimenter choose which group won yields few differences in in-group and out-group evaluations, having the groups choose heads or tails creates a striking bias toward the in-group (Rabbie & Horwitz, 1969). This line of research suggests that some form of competition may be necessary to generate discriminatory groups.

In summary, prominent social psychologists Sherif and Tajfel had stumbled on an interesting landmark of group formation in humans. Sherif believed that understanding the goals of the interacting groups was an important part of understanding the psychological mechanisms that occur during intergroup dynamics. Tajfel's theory of categorization emphasized that once an individual is associated or belongs to a different group (or category), the group is judged more differently (Tajfel & Wilkes, 1963). In an attempt to integrate these ideas, *social identity theory* emerged as a window into the processes that result in group formation (Tajfel & Turner, 1979). It proposes that social categorization helps to cognitively structure the world, but it also serves to provide motivation. An individual's social identity—her sense of who she is—is based in part on the group to which she belongs. Because individuals identify with certain groups, they also identify with the positively valued aspects of those groups. Thus, in order for an individual to maintain a positive self-evaluation, the individual must maximize the difference between his own group and others (the out-groups) in order to retain his positive social identity. In other words, the individual sees the positive in his own group and in turn discriminates against other groups (for instance, "Women are better than men!"; Tajfel & Turner, 1979).

Numerous studies have augmented the viewpoint that motivational and cognitive factors are important in intergroup processes. The processing of group-relevant information by group members, as opposed to mere observers, can be guided by an initial categorization based on in-group bias; a group member believes that the in-group is better than the out-group, unless there is strong conflicting evidence to the contrary (Maass & Schaller, 1991). Intergroup representations do not need to solely rely on perceptual features (e.g., a group labeled as "green" and a group labeled as "blue"), and categorization can occur at a more behavioral and ecologically valid level as well, such as identifying with a lower- versus higher-status group. For example, students in Switzerland who were preparing for university (high status) versus students who were undergoing vocational training (low status) did not exhibit much bias when encountering each other individually, but collectively encountering the other group significantly increased the discrimination toward the out-group (Doise & Sinclair, 1973). Intergroup discrimination can be found in children as young as age 7 years (Vaughan, Tajfel, & Williams, 1981) and seems to be related to an increase in self-esteem (Oakes & Turner, 1980). The positivity associated with an in-group seems to be a fairly automatic process, and simply referring to words that are associated with an in-group or out-group (e.g., "us" vs. "them") may unconsciously perpetuate these intergroup biases (Perdue, Dovidio, Gurtman, & Tyler, 1990).

As social psychological research became more sophisticated, new paradigms emerged to study this phenomenon. Rather than experimenters observing their subjects and taking overt measures, cross-cultural studies emerged and more subtle psychological measures were able to capture the automaticity of intergroup processes. For example, a group of researchers used an affective priming task in order to test whether assigning a social category to oneself is associated with some kind of positive in-group default (Otten & Wentura, 1999). In this masked priming task, a word that has been primed to be associated with either a positive (in-group) or a negative (out-group) valence is presented for a brief period of time (20 ms). The researchers found that during a minimal group paradigm, social categorization is sufficient to automatically and implicitly activate positive attitudes toward the category that was associated with the self. Although subjects showed an in-group favoritism effect, there was no negativity associated with the out-group, suggesting that out-group discrimination need not occur to have in-group favoritism.

Furthering the notion that the in-group facilitates positive self-evaluations, Smith, Coats, and Walling (1999) demonstrated that an individual's representation of the self overlaps with the representation of close partners and the in-group. Participants were asked to self-report on their characteristics and then evaluate either a close partner or an in-group member on their characteristics. The speed of response was faster for the close partner and in-group member when their characteristics matched those of the participants, facilitating the representation of the close partner and in-group member. Studies of minimal groups indicate that in-group favoritism exists across cultures, although the way in-group bias is expressed may be the product of the cultural value system (Wetherell, 1982).

Although the study of intergroup processes is complex, advancements in the field of social psychology, along with advancements in related fields such as social neuroscience, behavioral economics, and evolutionary anthropology, will allow researchers to continue to uncover the mechanisms by which groups are formed. The experimental approach utilized in social psychology is perhaps one of the most ecologically valid ways of studying group processes. By inducing individuals to form minimal groups, social psychologists are able to understand some of the psychological processes involved during group formation. However, as discussed previously, these highly variable techniques focus on psychological processes in populations that are traditionally studied in the lab. Cross-cultural studies promise to emphasize that intergroup processes are highly similar regardless of cultural differences. Moreover, using unconstrained nonlaboratory environments may elucidate processes that are not readily apparent in the typical experimental setup.

Moreover, experiments conducted in remote settings are prone to flaws. Individuals in these settings may exhibit behaviors that seem completely natural, but the power of social influence and the noise added by an observing experimenter may inhibit natural intergroup behaviors. Furthermore, social psychological research does not allow for a clear picture of the neural mechanisms involved in intergroup processes. Social neuroscience, an emerging field that aims to study how the brain instantiates social behavior, can provide valuable insights into the cognitive and affective processes underlying group dynamics. For example, one study demonstrates that the outcome of social group competition can directly affect brain systems involved with reward processing (Cikara, Botvinick, & Fiske, 2011). Simply having baseball fans view plays with negative or positive outcomes for their team triggered differential brain processing. A losing play was associated with activation in the anterior cingulate and insula (brain regions associated with internal conflict, pain, and negative affect), whereas a winning play was associated with activation in the ventral striatum (a brain region associated with reward). Combining cross-cultural studies with neuroimaging, one group has shown that there is cultural variation in brain responses associated with intergroup empathy and that this difference varies to the degree that the culture favors a social hierarchical structure (Cheon et al., 2011). Compared to American participants, Korean participants experienced greater subjective empathy and stronger activity in the temporoparietal junction when viewing in-group members in pain.

The study of intergroup processes in humans allows us to isolate human universals. However, complex intergroup processes occur in nonhuman primates as well. Understanding the evolutionary building blocks active during intergroup contexts will allow us to gain perspectives on how cultures develop and what they represent. Broadening the horizons of how researchers conceive of intergroup processes by combining human and nonhuman primate literatures and taking advantage of next-generation technologies will elucidate the mechanisms through which intergroup processes are based.

## Common: Group Distinctions Matter

Across the industrialized, small-scaled societies and nonhuman primate literature is the common theme that groups are relevant to social primates. This is not an obvious conclusion; other social variables, such as status or kin relationships, could easily dominate social behavior. Perhaps groups embody status and kin relationships, providing a simple heuristic for deciding which agents are likely to be helpful or harmful. Nonetheless, people are able to detect group differences and demonstrate prosocial behavior to perceived in-group members, sometimes even harming out-group members. This perception of group boundaries is a common cognitive component of intergroup behavior, leading to a cascade of affective responses that could be broadly construed as positive and negative. Anthropologists have been interested in the effects of the organization of society and the status of an individual in the society (see Douglas, 1970) and have suggested that communities can have many cultures, defined by comparing themselves against other cultures (Thompson & Wildavsky, 1990). This process can lead to cultural conflict. Affiliative behavior results from positive affect from in-groups, whereas sometimes violent and other harmful behaviors result from negative affect from out-groups. These universals across species suggest a fundamental construct in human psychology evolutionarily preserved for millions of years; culture simply determines the relevant groups and their standing relative to the cultural in-group.

## Redefining Culture

Given the scientific literature discussed so far, in concert with our broader approach to cultural neuroscience beyond brain imaging, human beings, and individual differences, the discussion places culture in a central position. Despite commonalities across species and industrialized and small-scale societies, there are many factors that distinguish these populations. Although these differences may be attributed to genetics and social context, culture captures a majority of this variability. However, traditional definitions of culture in social psychology do not allow for an explanation of these differences. There, culture is described by mutually exclusive categories communal and individualistic. Here, we propose a more inclusive definition of culture—a relevant social context in which group distinctions are salient. This broader definition of culture expands on theories that suggest common norms, celebrations, and language constitute separate cultures; instead, we argue that culture encompasses a much smaller collection of people than these traditional definitions allow. One possible interpretation of our definition is simply considering subcultures as cultures in and of themselves. By redefining culture in this manner, we are now able to better understand intergroup behavior. Because culture defines the relevant groups, knowledge of these groups and their dynamics constitutes membership within a culture if that knowledge governs interactions with those group members. For instance, children in a middle school have their own unique culture constituted with relevant groups that all citizens of the middle school, teachers included, are aware of and adjust their behavior to accordingly.

One obvious objection to this new definition of culture is that it is conflated with definitions of the social context. Surely *every* social context is not its own culture. If so, then how do we view groups who have formal institutions, languages, and other symbols representative of their culture? However, let's consider for a moment that every social context is indeed a unique culture. Such a consideration would force us to find common language, institutions, and symbols within each arbitrary social context. We argue that this is indeed possible if language is reduced to jargon, and institutions and other symbols to cognitive constructs. Let's return to the middle-school scenario. It is very common for members of a middle school to share a similar language. There are certain terms reserved for special events in the school calendar and certain words applied to particular behaviors that are unique to that context. Even if the events and behaviors are not unique, the terminology is probably so. Similarly, there are relevant cognitive constructs surrounding events, achievements, and accomplishments (e.g., detention) that facilitate the same functions of institutions. As such, by our relaxed definition, a middle school is a unique culture.

Another objection may be to speculate about what is gained by such a relaxed definition of culture. Surely considering a middle school as a social context should be sufficient, not necessitating the use of the reserved term culture. In response to this argument, we wonder, why not? Certainly nothing is lost by considering a middle school a culture, but we could potentially gain an alternative framework to explore behavior within that context. As such, making culture more inclusive promises to assist in a better understanding of social behavior shaped by culture. Next, we extend this consideration of culture to the hybrid field of cultural neuroscience, first discussing limitations of neuroscience approaches.

## Limitations of Current Neuroscience Approaches

The extended discussion of intergroup processes and culture forces a critique of current neuroscience approaches because of limitations. For instance, considering other species is but one tool of neuroscience, and access to the full toolbox would allow for better theory. Current neuroscience technology is expensive, obtrusive, and detracts from ecological validity. Therefore, studying culture with the available technology severely limits the complexity of inferences that can be made from the resulting data. Problems also result from highly variable technological approaches, experimental environments, and paradigms. If we are to observe more cross-cultural and cross-species commonalities, these obstacles must be resolved. Here, we examine how each limitation hinders generalization.

Variable technological approaches reflect the current evolution of brain science technology. Let us consider functional magnetic resonance imaging (fMRI) as an example. Although an advance on technology available 50 years ago, fMRI has already been around for 25 years. As such, it represents an older technological approach, with limitations that were acceptable at its onset but need to be overcome today if cultural neuroscience is to move forward. fMRI relies on blood oxygenation flow to detect a *correlate* of neuronal activity. It requires a magnetic field, no motion on the part of the participants, and generates enormous noise during data collection. As such, any experiment that employs this approach has sacrificed some degree of ecological validity, having their participants lie motionless in a loud, dark room.

Social behavior occurs in a rich environment on a day-to-day basis, and the processes that motivate such behavior are shaped by latent cultural factors not easily re-created in a laboratory environment, particularly a dark, loud environment in which participants must restrict their movement—all for a *correlate* of brain activity. This is not to say that the neuroscience of social behavior has not advanced because of the use of fMRI technology; rather, it is simply a comment that there is only so much we can learn with this technological approach. The field of neuroscience has long recognized this limitation, and recent technologies such as near-infrared spectroscopy overcome some of these setbacks while allowing for free motion, upright position, and laboratory environments more akin to the real world. Nonetheless, current neuroscience technologies available to cross-species and cross-cultural researchers are variable.

Because of the technological restrains, neuroscience experimental paradigms present the second major limitation. As mentioned previously, culture occurs with a specific context; as such, re-creation of those contexts is crucial for eliciting ecologically valid behavior. Researchers have always been clever at creating such context, but neuroscience technologies make this a more daunting challenge. Even without the neuroscience technologies, experimental context must satisfy experimental, psychological, and mundane realism—the extent to which events occurring in the laboratory are likely to occur in the real world. Mundane realism can be achieved through simple creativity by providing participants as real or ecologically valid a context as possible. For instance, if researchers want to study the communication of contempt in cross-cultural romantic interactions, they may ask potential participants to bring their romantic partners to the study. Therefore, the interaction being explored achieves mundane realism because they are actual real-world interaction partners. However, the achievement of this realism does not satisfy demand effects.

Experimental realism describes the situation as involved; participants must take the situation seriously, and it must have an impact on them. Because the experiment is in an artificial environment, experimental realism is particularly important and very much depends on the theatrical nature of experimental social psychology. Consider economic games as an example. Experimental realism is evident in that if someone is unfair toward you in the context of the game, your psychological experience is real and impactful. In contrast, a common failure of experimental realism is that in anonymous, one-shot games, subjects still behave as if they are being observed—even an irrelevant picture with a pair of eyes hanging on the wall can increase prosocial behaviors (e.g., Bateson, Nettle, & Roberts, 2006).

Related to experimental realism is psychological realism; the psychological processes that occur in real life should occur in the experiment. Staying with our unfairness example, the psychological experience of being treated unfairly is likely the same inside and outside of the experimental setting. Therefore, realism allows experimenters to compensate for the controlled yet artificial environment of the laboratory. However, this is harder to achieve across species; since other species cannot (or will not) play such economic games amongst themselves, we cannot make a similar comparison. Behavior in economic games with human experimenters is only marginally comparable to their evolved everyday psychological reality.

However, the goal of each experiment is not necessarily to be applicable to real-world phenomena. Sometimes experiments are used to test theories—a perfectly valid motivation for experimentation. In our opinion, hybrid fields such as cultural neuroscience play a vital role in this aspect of science because they can help dissociate a myriad of theories for specific social behaviors. Nonetheless, many classic experiments simply rule out alternate explanations for behavior. For example, the emotions literature posited two competing hypotheses for the relation of cognition and affect; the James–Lange theory (Lange & James, 1922) states that biological feedback from muscle contraction and autonomic systems constitutes emotion, whereas Cannon's (1927) objection stated that visceral sensations were too diffuse and the autonomic system to slow to successfully constitute emotion. One experiment aimed at teasing these two hypotheses apart asked participants to hold a pen in their lips, inhibiting a smiling facial expression, and then judge the humorousness of cartoons (Strack, Martin, & Stepper, 1983). These researchers found that participants with the pens found the cartoons less humorous. Although people do occasionally put pens in their mouths, this experiment is not particularly relevant to real-world phenomena. However, it did provide support for the James–Lange theory because it suggested that interference of facial muscles changed the ability of participants to experience emotion.

In summary, cultural neuroscience faces a quandary when asked to create experimental paradigms that facilitate the collection of neuronal and physiological data. Culture inhabits rich, naturally occurring environments—environments that must be constrained by the limitations of neuroscience technologies. As such, researchers strive to attain realism to truly capture the complex phenomena under investigation.

## Next-Generation Sensors

Currently, no technology exists that allows neural and physiological recordings in naturalistic settings. Next-generation technology has the potential to provide data in an ecologically valid manner across a variety of human populations and species through the development of a miniscule, portable, wireless neurophysiology sensor package. Moreover, this technology could facilitate comparison across population and species, allowing researchers to make inferences about human nature and the effect of culture on social behavior. This next-generation sensor package could capitalize on cutting-edge research in nanotechnology, utilizing unique signal processing algorithms to provide instantaneous neurological and physiological information from a variety of populations, providing a more complete picture of central and peripheral nervous system functioning across populations and species. This informationwill improve understanding of social behavior. In addition, if next-generation sensors can allow for unobtrusive recordings, they will controll for demand characteristics and experimenter effects. Therefore, these next-generation sensor packages have the ability to revolutionize cultural neuroscience by allowing researchers to understand human brain function across various ecological contexts, age groups, and species and to understand the origin and constraints of brain function.

## Implications for Global/Population Health

Intergroup conflict is one of the largest public health concerns throughout the world. Up to 14% of human death in prehistory was a result of warfare (Walker & Bailey, 2013). At least 40 people are murdered each day in the United States. In the twentieth century, genocide accounted for hundreds of millions of deaths. From open conflicts that range from civil unrest, gang violence, and tribal disputes to more large-scale conflicts between nations and ideologies, the threat of mankind's destruction by its own hand has not ceased. The research on intergroup behavior in social psychology has not stemmed the tide of intergroup conflict that has plagued mankind since earliest records were kept. This failure does not result from a lack of sensible theory; rather, it can be attributed to highly complex phenomena with variable causes from context to context. Cultural neuroscience harbors the possibility of a resolution to intergroup conflict by combining research on culture with brain sciences. This simultaneously allows for an understanding of these complex cultural phenomena with accompanying psychological and neurological mechanisms. However, a new, more specific definition of culture is necessary before real breakthroughs in intergroup conflict can be realized. This must be accompanied by next-generation neuroscience technology to facilitate a common metric across cultures and species. Then, perhaps, cultural neuroscience can realize its potential to eradicate intergroup conflict.

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# CHAPTER 17

# The Cultural Neuroscience of Intergroup Bias

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**Abstract**

Culture defines how groups, and the individuals situated within them, conceptualize and navigate relationships with in-group and out-group members. How diversity in these group processes and their neural substrates emerge remains an open question. Diversity in intergroup processes may have arisen from perceived threats from the environment. Groups in environments that present greater collective uncertainties and threats may have been more likely to adopt shared norms, practices, and institutions that promote and reinforce cohesion, coordination, and the prioritization of the welfare of in-groups over out-groups—contributing to cultural diversity in intergroup bias. This cultural diversity is proposed to be supported by differential pressure across environments on neurobiological systems that regulate responsiveness to threats and facilitate affiliation with in-groups. These two processes may mutually reinforce and co-construct one another, functioning to translate perceived threats from the environment into the cultural variations observed in the neural and behavioral manifestations of intergroup bias.

**Key Words:** gene × environment, prejudice, discrimination, intergroup conflict, bias

In a rapidly globalizing and diversifying world, harmonious intergroup relations and cooperation within and across societies are more necessary than ever. According to projections, within the United States, Whites will no longer be a majority racial group by the year 2043 (U.S. Census Bureau, 2012). On a global scale, immigration is increasing and migrants are being more widely distributed across nations (United Nations, 2009). However, we live in a world that is not only becoming more interconnected but also appears at times to be more uncertain, chaotic, and dangerous. Economic hardships, political unrest, unpredictable violence, intense natural disasters, and deadly new strains of infectious diseases are just some of the threats that we are reminded of on a daily basis through the news, media, or personal experience. Unfortunately, increased intergroup exposure and heightened perceptions of threat may be two key ingredients for intergroup tensions and biases. In a society marked by diversity, systematic intergroup biases can form the basis for divisions and pernicious social problems, such as prejudice, discrimination, and intergroup conflict.

In this chapter, we explore the role of perceived threat as one critical mechanism that shapes group processes across cultures. By perceived "threat," we refer to a broad, yet interrelated, pattern of subjective experiences marked by feelings of anxiety, fear, uncertainty, and vulnerability in response to the obstruction of fundamental psychological needs. Situations that undermine and disrupt basic psychological needs, such as security, belonging, control, meaning, and epistemic needs, are typically perceived to be threatening and elicit subjective states of uncertainty and anxiety (Greenberg, Solomon, & Pyszczynski, 1997; Hogg, 2007; Kay, Whitson, Gaucher, & Galinsky, 2009; van den Bos, 2009).

Our proposed framework is based on the central idea that threats provoke adaptive responses at the social, psychological, and neurobiological levels (Figure 17.1). This framework is based on the following premises, which are discussed in further detail in the following sections of the chapter. The first premise is that the subjective experience of threat elicited by environmental pressures shapes how individuals organize and structure their relationships with others, especially group members. Specifically, such threats are predicted to promote greater levels of social cohesion, structure, order, and coalition within groups and organizations. Historical and regional variations in recurring or chronic stressors may form a basis for cultural diversity in cultural practices and norms that mobilizes and maintains social cohesion. The second premise is that exposure to such threats may also heighten and facilitate psychological and associated neurobiological processes involved in recognizing, regulating, and responding to threat. Finally, we propose that the interplay of cultural systems that promote social cohesion and psychological/neurobiological systems of threat management may shape group processes.

This chapter is organized according to the premises of our proposed framework (see Figure 17.1). First, we explore ways in which perceived threats may act as a pressure for social cohesion and the adoption of more cohesive, coordinated, and ordered forms of sociality. Next, we examine how diverse manifestations of historical and recurring environmental/ecological threats may influence cohesive patterns of social organization and indirectly shape intergroup bias. We next propose some candidate neurobiological and genetic mechanisms that may facilitate intergroup bias as a function of threats and the demands of the cultural environment. Finally, we explore the relationship between the threat experienced within intergroup contexts and health-related risks.

## Threat and Cultural Diversity of Group Processes

Defining "culture" can be a challenging, complex, and controversial endeavor. Here, we conceptualize culture as a shared system of meanings, knowledge, practices, and norms among a group of interconnected people. Of particular relevance to this chapter is the adaptive function of shared meanings, practices, and expectations for interconnected individuals. One defining functional characteristic of culture is to allow for dynamic adaptations of interconnected individuals to the demands of shared physical and social environments (Boyd & Richerson, 1985; Chiao, Cheon, Porntattananangkul, Mrazek, & Blizinsky, 2013; Cohen, 2001; Triandis, 2009). Socioecological approaches to understanding cognition and behavior (see Oishi & Graham, 2010; Fincher, Thornhill, Murray, & Schaller, 2008; Triandis, 2009) provide insights into how cultural variations in values, norms, social organization, and individual psychological processes may arise from historical pressures induced from both natural and social habitats and ecologies. Although different features of ecologies and physical environments may be associated with diverse cultural dimensions and syndromes (see Triandis, 2009; Hofstede, 2001), one broad means in which local ecological demands may influence social organization is through eliciting cultural practices and norms that exert cohesiveness and coordination among group members.

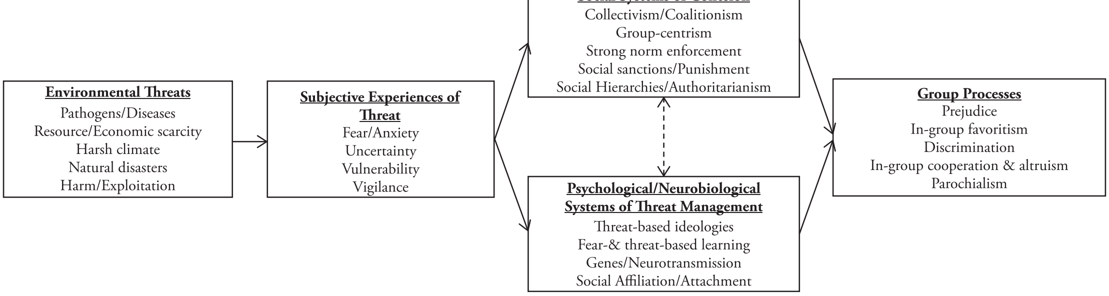

**Figure 17.1** Schematic overview of how cultural diversity in group processes (and the social, psychological, and neurobiological mechanisms regulating these processes) could arise as an adaptive response to shared external threats. The dotted bidirectional arrow represents the mutually reinforcing relationship between social systems promoting cohesion and the psychological/neurobiological mechanisms regulating detection and responses to threats.

As an obligately interdependent species (see Brewer, 2004; Caporael & Brewer, 1995), human beings must rely on codependent sociality and group living as primary adaptations for survival. Individual psychological and behavioral tendencies are largely adapted to the demands of the group, and they are indirectly shaped by environmental pressures (Brewer, 2004; Caporael, 2007). As such, group survival hinges on the ability of group members to effectively cooperate, coordinate, and mobilize efforts to overcome common threats and challenges (Boyd & Richerson, 2009; Gintis, Bowles, Boyd, & Fehr, 2003; Navarrete & Fessler, 2005). Consequently, variations in recurring threats and pressures across environments may require groups to adopt differing patterns of social organization, norms, and practices (Cohen, 2001; Nisbett, 2003; Triandis, 2009).

Social systems that promote cohesion and coordination may have been especially necessary or optimal in the face of shared external environmental threats. However, there are diverse solutions or equilibrium states that may allow groups to achieve necessary cohesion and coordination (see Cohen, 2001). One potential system that may satisfy such external demands for cohesion is collectivism, in which the self is defined by relationships with group members and close others (Brewer & Chen, 2007). On the one hand, collectivistic values and norms emphasize interdependence, loyalty, conformity, and fulfilling obligations to one's in-group and common goals (Oyserman, Coon, & Kemmelmeier, 2002; Triandis, 1995). On the other hand, social organization into hierarchies or under the guidance of an authority may be another system of organization that produces cohesion and coordination. Hierarchical (relative to egalitarian) values and practices stratify status and power within groups, and they provide clear and salient expectations about the relationships between those with low and those with high power (Hofstede, 2001). Hierarchies also provide coordination of resources and reduction of uncertainty among group members through specialization of roles and responsibilities (Magee & Galinsky, 2008; Sidanius & Pratto, 1999). Finally, group cohesiveness and coordination may also be achieved through ensuring strict socialization and adherence to shared norms. Tight (relative to loose) cultures involve social systems that strictly enforce norms and harshly sanction deviants and those counterproductive to such norms (Gelfand et al., 2011). Similarly, anthropological perspectives from the cultural theory of risk have also emphasized the role of external hazards on sensitivity to violations of societal norms and social structuring (Douglas, 1992). Consistent with the importance of norm enforcement for fulfilling coordination needs, behavioral economic studies on "strong reciprocity" (see Bowles & Gintis, 2000) have revealed that not only cooperation but also the willingness to engage in punishment of non-cooperators and deviants may be necessary to sustain cooperation within groups (Fehr & Gachter, 2002).

In other words, dispositions and behaviors that may undermine group cohesion and coordination may have been liabilities for group success in environments that presented chronic hazards, stressors, and uncertainties. Instead, cultural values and social institutions that promoted the independence of the self, pursuit of individual aspirations over collective goals, and permissiveness of non-normative behaviors may have been luxuries afforded by relatively safer and predictable environments or during prolonged periods of relative security and stability.

Indeed, cross-national and cross-regional findings suggest that such cultural systems that promote coordination, cohesion, or structure among group members may be more prevalent in environments and regions that have had greater histories of chronic or recurring external threats. Threats and uncertainties may promote stronger motivations to establish shared worldviews; identify with in-groups; and mobilize coalitional cohesion, cooperation, and consensus (Greenberg, Solomon, & Pyszczynski, 1997; Hogg, 2007; Kruglanski, Pierro, Mannetti, & De Grada, 2006; Navarrete & Fessler, 2005; Navarrete, Kurzban, Fessler, & Kirkpatrick, 2004). Consequently, local ecologies and environments that present greater threats or pressures for social cohesion may also produce norms, values, and practices that may promote and reinforce stronger identification and prioritization of in-groups relative to other groups. Although related, these cultural systems that promote cohesion may be adopted independently of one another and may be adopted according to different contextual preconditions. For example, whereas collectivism is associated with national wealth, tightness appears to be less sensitive to national wealth indicators (Gelfand et al., 2011).

Ultimately, diversity in local environmental threats and the associated demand for in-group cohesion and affiliation may act as one basis for cultural diversity in group processes. Consistent with this notion, culturally shared values, norms, and stereotypes define the boundaries and permeability of group memberships (Yuki, Maddux, Brewer, & Takamura, 2005; Yuki & Schug, 2012), as well as dictate the specific groups that should be avoided or stigmatized (Levy, West, Ramirez, & Karafantis, 2006; Yang et al., 2007). The stigmatization, avoidance, and exclusion of out-groups and individuals who pose threats to the group may have been a universally adaptive feature of groups (Cottrell & Neuberg, 2005; Kurzban & Leary, 2001; Oaten, Stevenson, & Case, 2011). However, the qualities and characteristics perceived to be deviant or disruptive to optimal social relations and group functioning may be defined by local cultural values and social meanings (Yang et al., 2007). For instance, within a culture or social system that values conformity, uniqueness or nonconformity may be interpreted as deviance and negatively interpreted (Kim & Markus, 1999). Similarly, within a culture that highly values prosperous continuation of family lineage (i.e., the Chinese), groups that pose culture-specific threats to this goal, such as people with mental illness, may be especially stigmatized and excluded from social relations (Yang et al., 2013).

Here, we review previous studies that demonstrate the role that diverse manifestations of environmental and ecological threats (and sensitivity to such threats) may have on the adoption of cultural systems that promote cohesive and structured social organization, as well as intergroup attitudes and conduct.

### *Pathogenic/Disease Threats*

One ecological threat that has received much attention in the study of group processes, as well as cultural diversity, is pathogens. Pathogens have existed as a recurring threat to both survival and reproduction, and as such, they may promote psychological, behavioral, and group-oriented adaptations to minimize the contraction and spread of pathogenic infection (Kurzban & Leary, 2001; Schaller & Park, 2011). According to intergroup vigilance theory and behavioral immune system perspectives on intergroup bias (Oaten, Stevenson, & Case, 2011; Schaller & Park, 2011; Schaller, Park, & Faulkner, 2003), one evolutionary mechanism for wariness and prejudice toward out-groups involves the threat of infection by communicable pathogens from out-groups. Consequently, appearance, customs, mannerisms, and practices that may appear foreign or deviant from in-group norms may have served as cues of communicable pathogens in ancestral environments and elicited reactions of anxiety, disgust, and aversion (Cottrell & Neuberg, 2005; Kurzban & Leary; 2001; Park, Faulkner, & Schaller, 2003; Schaller & Park, 2001; Schaller, Park, & Faulkner, 2003). Ultimately, in contemporary society, out-group members associated with potential cues of infection may elicit negative emotions of fear and disgust and may motivate avoidant and discriminatory behavior.

Accordingly, regions of the world that have faced greater historical prevalence of pathogenic threats include populations that tend to exhibit greater affiliative and cohesive proclivities toward their in-group. For instance, Fincher and colleagues (2008) utilized epidemiological records to reveal that historical prevalence of pathogens threatening to human reproductive fitness was positively correlated with indices of collectivism cross-nationally. Subsequent studies have similarly determined that regional pathogen prevalence is predictive of greater levels of conformity to norms (Murray, Trudeau, & Schaller, 2011) and greater endorsement of socially binding moral foundations, such as in-group loyalty, authority, and purity (van Leeuwen, Park, Koenig, & Graham, 2012). Consequently, activation of infection concerns also evokes stronger distinctions between in-group and out-group in attitudes and behavior. For instance, when exposed to reminders of how easily germs can proliferate and spread in daily life or messages regarding the threat of outbreaks, participants are less likely to support immigration of unfamiliar, relative to more familiar, immigrant groups into their country (Faulkner, Schaller, Park, & Duncan, 2004) and are more likely to associate disabled and obese people with infectious traits (Park et al., 2003; Park, Schaller, Crandall, 2007).

Just as environmental cues of infection threats may also promote greater intergroup biases toward foreign immigrants, individual differences in psychological sensitivity or concern regarding infection also moderate biases against infection-signaling out-groups, such as the physically disabled or immigrants from culturally unfamiliar countries (Park et al., 2003; Schaller, Park, & Faulkner, 2003). Even being in a state of increased biological susceptibility to pathogens, such as the first trimester of pregnancy, may lead to elevated ethnocentrism (Navarrete, Fessler, & Eng, 2007). Conversely, receiving immunizations from contagious diseases can lead to attenuated bias against out-group members (Huang, Sedlovskaya, Ackerman, & Bargh, 2011), perhaps by providing a psychological buffer against the threat of infection and the consequent intergroup bias.

### *Climate-Related Threats*

Climate has been linked to shaping diverse social processes, such as violence and aggression (Anderson, Deuser, & DeNeve, 1995), and individualistic–collectivistic tendencies (Hofstede, 2001). Regional climatic variations have also been linked to intergroup perceptions and attitudes. Specifically, van de Vliert (2011) revealed that the relationship between harshness of climate, indexed by temperatures with greater deviations from a temperate climate (i.e., very hot summers and/or very cold winters), and in-group favoritism across nations was moderated by national resources (national wealth). Whereas in lower-income countries, harsher climates were associated with greater levels of in-group favoritism for countrymen (vs. immigrants) and relatives (vs. nonrelatives), this relationship was not observed in higher-income countries, suggesting both the role of climactic threats and the presence of resources against these ecological demands may shape intergroup conduct within societies.

### *Harm/Exploitation*

Given that out-groups may have been historically associated with threats related to harm and exploitation, psychological mechanisms for vigilance and avoidance of others who are marked with a "tribal" stigma (see Goffman, 1963; Kurzban & Leary, 2001), such as race, nationality, religion, and unfamiliar customs, may have served as an adaptive function for both individual and group survival. Our ancestral past involved a period of living in tribal units in which intertribal competition, conflict, and exploitation may have been prevalent (Schaller, Park, & Faulkner, 2003). Indeed, archaeological and anthropological evidence suggests that ambushes and raids between hunter–gatherer tribes were a significant and common survival threat, even with enough intensity to have potentially acted as a selection pressure on within-group altruism and cooperation among prehistoric humans (circa late Pleistocene and early Holocene eras) (Bowles, 2009). Paralleling this notion in the modern era, greater historical instances of territorial conflicts or invasion from neighboring states have been associated with greater adoptions of tight cultural norms (Gelfand et al., 2011).

One's working models and expectations about vulnerability to threats from others in the social environment may also moderate processes underlying intergroup bias. Based on prior experience or social learning, individuals who perceive greater likelihood of harm and exploitation by others may exhibit greater biases toward members of groups that signal or are heuristically associated with threat. For instance, those who maintain such perceptions of threat from the social environment, as indexed by stronger beliefs in a dangerous world, are more likely to categorize ambiguous but threat-cuing targets as out-group members (Miller, Maner, & Becker, 2010). Furthermore, those who endorse beliefs in a dangerous world also exhibit greater stereotyping of out-group members on dimensions related to threat and danger, especially when exposed to environmental cues that elicit feelings of vulnerability, such as ambient darkness (Schaller, Park, & Mueller, 2003). At a national level, threats and biases toward out-groups may be moderated by perceptions of their criminality and danger to security. Right-wing authoritarianism (RWA), which reflects social attitudes and ideologies valuing submission to authority and strict adherence to traditional norms grounded on perceptions of a dangerous world (Altemeyer, 1988; Duckitt, Wagner, Plessis, & Birum, 2002) was observed to be particularly predictive of anti-immigrant attitudes in countries in which immigrants were perceived to contribute to the crime rate (Cohrs & Stelzl, 2010).

More generally, being in states of biologically or hormonally mediated sensitivity or vulnerability to harm may elicit greater intergroup bias associated with vigilance or wariness toward out-group members. Elevated periods of fertility during women's menstrual cycles are associated with greater levels of risk aversion and avoidance of risky and potentially dangerous situations (i.e., taking out garbage in the evening, inviting a man for a coffee after a date, or parking in a dark corner) (Broder & Hohmann, 2003). Given that risks and consequences of sexual coercion would be substantially greater when fertility is high, women may generally experience higher sensitivity to potential threats, especially threats from unfamiliar males, during periods of elevated fertility. Accordingly, states of peak fertility are also associated with greater levels of intergroup bias toward males of both racial and minimally defined out-groups, especially when these males are perceived to be physically formidable or fear of sexual coercion is high (McDonald, Asher, Kerr, & Navarrete, 2011; McDonald, Navarrete, & Van Vugt, 2012; Navarrete, Fessler, Fleischman, & Geyer, 2009).

### *Competitive/Economic Threats*

Similarly, intergroup competition for scarce resources and opportunities may also have served as a historical impetus for intergroup bias and conflict. In modern societies, out-groups may often be perceived as sources of potential competition and conflict over resources and opportunities. Perceived competition may elicit hostility and distrust toward members of such out-groups, as well as greater cooperation and coalitionism within groups (Bornstein & Ben-Yossef, 1994; Levine & Campbell, 1972; Sherif & Sherif, 1969; Wildschut, Pinter, Vevea, Insko, & Schopler, 2003). Ecological and environmental pressures that signal paucity of resources may heighten perceived competitive threats from out-groups that exacerbate intergroup bias. For instance, merely activating concepts of resource scarcity (vs. abundance) through images signaling economic hardships has been associated with less inclusiveness and reduced likelihood of categorizing ambiguous targets (i.e., biracials) as in-group members (Rodeheffer, Hill, & Lord, 2012). Furthermore, when scarcity of resources or opportunity is salient, greater intergroup biases and reduced prosociality may be exhibited toward groups perceived as more competent competitors, such as immigrants portrayed to be successful in a tough job market (Esses, Dovidio, Jackson, & Armstrong, 2001).

## Cultural Neuroscience of Threat and Group Processes

In the previous section, we explored how ecological and environmental threats may promote systems of sociality involving more clearly defined, cohesive, and coordinated groups—ultimately promoting cultural diversity in social environments. However, chronic exposure to such threats may also mobilize and heighten a profile of psychological responses involved in the recognition, response, and regulation of such threats. The neurobiological substrates of such threat-management processes may also undergo changes over time, which may eventually shape cognition, attitudes, and behavior across individuals and cultures as a function of threat.

Cultural neuroscience seeks to explore such questions pertaining to bidirectional relationships, or the mutual construction, of culture and the brain (Chiao & Ambady, 2007). The relationship between cultural and neurobiological processes can occur across multiple timescales, ranging from situational influences, within a lifespan, to across generations (Chiao et al., 2013). Societies and social environments vary in recurring everyday situations that individuals encounter, which shape the mind by heightening accessibility of knowledge, schemas, procedures, and goals chronically activated by such recurring situations (see Gelfand et al., 2011; Hong, Morris, Chiu, & Benet-Martinez, 2000). Psychological responses to recurring situational demands may also be reflected by changes to neurobiological processes, such as changes in hippocampal volume as a function of recurring demands for complex spatial navigation and memory (Maguire et al., 2000).

Our framework proposes that external threats may contribute to more cohesive patterns of social organization (culture), as well as changes in the neurobiological systems involved in recognizing and regulating threats (brain). Social systems and structures facilitating group cohesion and coordination in response to threats may exert a bidirectional or mutually sustaining relationship with psychological (and associated neurobiological) mechanisms that heighten sensitivity, reactivity, and regulation of threats (dotted line in Figure 17.1). Prior research examining the relationship between social organization of groups and the structural organization of the brain provided initial evidence of this coevolution or mutual construction of the brain and culture to external demands and threats. The social brain hypothesis (see Dunbar, 1998) suggests that brains have been adapted to resolve problems associated with social ecology and group living, particularly the demands of navigating more complex and uncertain social worlds. For instance, species living in more complex social arrangements (e.g., living in larger group sizes) tend to exhibit larger brain relative to body sizes (Pérez-Barbería, Shultz, & Dunbar, 2007). Similar phenomena have also been observed in humans, albeit more selectively within specific regions of the brain. Increasing complexity of social relationships and networks has been selectively associated with increased volume of the amygdala but not other subcortical structures, reinforcing the significant role this structure plays in the identification of conspecifics and socially situated motivational cues (Bickart, Wright, Dautoff, Dickerson, & Barrett, 2010). Furthermore, life in denser and more chaotic urban environments, compared to less socially dense and complex environments, has also been linked to heightened reactivity of the amygdala during socially stressful tasks

(Lederbogen et al., 2011). Ultimately, the interplay between these social and neurobiological adaptations to external threats may jointly influence group processes across cultures. Here, we outline a number of such candidate threat-relevant psychological (and associated neurobiological) mechanisms that may contribute to cultural diversity in group processes.

### *Threat-Based Ideologies*

Like culture, ideology can be a difficult concept to define. Jost, Frederico, and Napier (2009) offer definitions of ideology as "a set of beliefs about the proper order of society and how it can be achieved" (Erikson & Tedin, 2003, p. 64) or as "the shared framework of mental models that groups of individuals possess that provide both an interpretation of the environment and prescription as to how that environment should be structured" (Parsons, 1951, p. 24). As a component of culture, ideologies reflect systems of beliefs about the social world that are shared among interconnected individuals (e.g., individuals with similar political orientations). Likewise, ideological beliefs prescribing social cohesion, coordination, and order may arise from heightened experiences of threat and motivations to fulfill psychological needs (Jost & Amodio, 2012; Jost et al., 2009; Jost et al., 2007).

Among the most prominently studied ideologies associated with threat and sensitivity to negativity are the interrelated belief systems of political conservatism, RWA, and social dominance orientation (SDO). Both conservatism and RWA encompass beliefs and values that support and promote social order based on underlying motivational concerns and worldviews pertaining to threat, uncertainty, and danger (Dodd et al., 2012; Duckitt et al., 2002; Hibbing, Smith, & Alford, 2014; Jost, Glaser, Kruglanski, & Sulloway, 2003; Jost et al., 2007). Although SDO is not typically considered to be a product of general sensitivity to threats or a negativity bias (see Hibbing et al., 2014; Pornpattananangkul, Cheon, & Chiao, 2014), it is associated with perceived threats specifically pertaining to competition, status, and scarcity of resources and opportunities, as indexed by an underlying "competitive jungle" worldview and perceived zero-sum relations between individuals and groups (Duckitt & Sibley, 2009; Sidanius & Pratto, 1999). Thus, although SDO may not be conventionally associated with threat and security-related worldviews, we refer to SDO as a threat-based ideology in this chapter given the influences that economic, status, and competitive threats have on shaping intergroup processes (see Riek, Mania, & Gaertner, 2006; Stephan & Stephan, 2000).

Importantly, the adoption and defense of these threat- and competition-based ideologies may be important psychological mechanisms underlying cultural systems that promote social cohesion, coalitionalism, and order. Paralleling the values promoted by cultural tightness at a societal and organizational level, political conservatism and RWA endorsed by individuals consists of attitudes and beliefs supporting the defense of traditional values and norms and harsh sanctions of deviants and offenders who violate such norms (Altemeyer & Zanna, 1998; Jost et al., 2003). Similarly, just as cultural systems may adopt hierarchical rather than egalitarian relations in response to coordination needs (see Sidanius & Pratto, 1999), ideologies based on threat-related motivations may consist of hierarchical and less egalitarian worldviews. Accordingly, political conservatism, RWA, and SDO also consist of prescriptive beliefs supporting social hierarchies, such as justifying or legitimizing status inequalities between groups or supporting deference to authority figures and strong leaders (Altemeyer & Zanna, 1998; Halabi, Dovidio, Nadler, 2008; Jost et al., 2003; Sidanius & Pratto, 2001).

Moreover, such threat-related ideologies are also predictive of individual differences in prejudice and intergroup bias. Allport (1954) concluded that "prejudice is basically a trait of personality. . . . The object of prejudice is more or less immaterial" (p. 71). Supporting Allport's observation, the interrelated and threat-based ideologies of conservatism, SDO, and RWA have been consistently associated with intergroup bias directed at diverse out-groups. When used to predict prejudice toward a variety of out-groups, the two measures predicted a total of roughly 50% of the variance across distinct prejudice measures, leading Altemeyer and Zanna (1998) to conclude that prejudices are "largely matters of personality and only two kinds of personality are basically involved: the social dominator and the right-wing authoritarian" (p. 60).

Such ideological beliefs may modulate how the brain processes information, particularly in intergroup contexts. Higher endorsement of SDO has been associated with lower levels of empathy (Pratto, Sidanius, Stallworth, & Malle, 1994). Work by Chiao, Mathur, Harada, and Lipke (2009) extended these findings to examine the modulation of neural empathic responses to the suffering of others by SDO. The authors observed a negative relationship between SDO and activity in the anterior cingulate cortex and the left anterior insula—regions involved in processing pain-related stimuli—when participants viewed scenes depicting the suffering of others relative to neutral scenes. In other words, those endorsing higher levels of SDO exhibited lower levels of activity in regions involved in empathic and pain-related processing to the suffering of others.

Cheon and colleagues (2011) further explored these mechanisms in the context of cultural preferences for hierarchical social relations and intergroup empathic biases. In this cross-cultural functional neuroimaging study, the authors recruited participants from a culture exhibiting relatively greater hierarchy-related values and practices (i.e., South Korea) and a culture exhibiting relatively lower levels of hierarchical practices (i.e., European Americans in the United States) (see Hofstede, 2001). During functional magnetic resonance imaging (fMRI) scanning, participants were shown scenes of respective in-group and out-group members (e.g., other Koreans or European Americans) in mundane or emotionally painful situations, such as in the midst of a natural or man-made disaster. Participants also provided a rating of their empathy toward the targets of each scene and completed the SDO scale as a measure of preference for social hierarchies. The authors found an in-group favoritism in neural empathic responses such that the temporoparietal junction (TPJ), a region involved in inferring mental and emotional states of others (see Saxe & Kanwisher, 2003), was more responsive to the suffering of in-group members relative to out-group members. Although this in-group favoritism in TPJ response to the suffering of in-group members was observed for both Korean and American participants, the selective TPJ response was stronger among Korean participants relative to the American participants. Paralleling the findings of Chiao and colleagues (2009), SDO was associated with greater levels of empathic intergroup bias reflected by greater empathy ratings for in-group suffering and greater selective reactivity of the left TPJ to the suffering of in-group members. Moreover, the relationship between SDO and self-reported intergroup empathy bias was mediated by selectivity in left TPJ response to the pain of in-group relative to out-group members. Given that Korean participants exhibited greater preferences for social hierarchy and intergroup empathy bias than American participants, these findings support the notion that ideologies and preferences for hierarchical social order (which are more prevalent in relatively hierarchical cultures) may be predictive of greater selective sensitivity to the suffering and needs of in-group members in situations that demand coordination and cooperation in response to external threats (i.e., a disaster).

### *Threat-Based Social Learning*

Another mechanism that may be useful for understanding the links between environmental threats, culture, and intergroup processes concerns the mechanisms underlying social learning. Implicit and nonverbal social learning mechanisms, such as imitation, mimicry, and both operant and associative forms of conditioning, function as mechanisms for the transmission and inheritance of cultural norms (see Bandura & McClelland, 1977; Boyd & Richerson, 1985; Weisbuch & Ambady, 2008). Such social learning mechanisms can also involve motivational value, reinforcement, or contingencies based on threats, such as in fear conditioning or the use of punishment in instrumental learning (see Seymour, Singer, & Dolan, 2007). As noted previously, punishment or associating maladaptive responses with negative outcomes may have been a critical component for sustaining and encouraging group cooperation and coordination (Fehr & Gachter, 2002; Gintis et al., 2003). Furthermore, mechanisms to readily and automatically recognize the fear expressions of conspecifics and group members to potential hazards would have provided a survival advantage in the context of group living. The bilateral amygdala (a structure involved in detecting fear expressions) exhibits greater reactivity to the fear expressions of members of one's own cultural/ethnic group compared to out-group members (Chiao et al., 2008). Moreover, both humans and primates exhibit abilities for vicarious fear conditioning, in which novel events and objects may be indirectly associated with fear and threat after viewing others' fearful reactions to the target (Crişan et al., 2009; Mineka & Cook, 1993; Olsson, Nearing, & Phelps, 2007).

One particular form of social learning that may be especially relevant to culture and intergroup bias is evaluative conditioning. Evaluative conditioning serves as one critical means by which individuals acquire attitudes and preferences toward new objects and people (Hoffmann, De Houwer, Perugini, Baeyens, & Crombez, 2010; Olson & Fazio, 2002). In particular, evaluative conditioning (particularly for fear) may have played a key role in the proper socialization and learning of social and moral norms. Psychopaths, for instance, have been identified to exhibit deficient conditioned fear responses and attenuated responses in the neural circuitry involved in fear-based learning (Birbaumer et al., 2005; Blair, 2007). With regard to in-group bias, evaluative conditioning may be one mechanism in which negative biases and stereotypes against out-groups may be acquired, either through personal experience or through social learning of the notion that out-groups are a source of threat and should be feared, avoided, or distrusted. In the case of prejudice, when an individual is consistently exposed to representations of a social group (e.g., African Americans) and negative evaluative descriptions about the group (e.g., dangerous and unpleasant) from the cultural environment, the group and the evaluation become associated in memory, leading to negative affective reactions during future encounters with individuals who belong to the out-group (Amodio, Devine, & Harmon-Jones, 2008; Fazio & Olson, 2002). Fear responses may also be especially readily conditioned and associated with faces of out-group males, who heuristically signal threat, and such conditioned responses may be more resistant to extinction compared to conditioned fear responses for in-group members (Navarette et al., 2009; Olsson, Ebert, Banaji, & Phelps, 2005).

These conditioned responses acquired from the broader social–cultural milieu may be activated automatically and can influence behavior toward out-groups even without intention or conscious awareness (Bargh, 1994; Greenwald, McGhee, & Swartz, 1998). Supporting this notion, prolonged exposure to news coverage reporting violent crimes of African Americans has been observed to facilitate adoption of more negative and threat-related evaluations of African Americans (Dixon, 2008; Gilliam & Iyengar, 2000). Similarly, racial biases may also be communicated implicitly and subtly through television programs. Such implicit cues include nonverbal facial expressions and gestures of characters that subtly signal disfavor toward racial out-group characters (Weisbuch, Pauker, & Ambady, 2009). Greater exposure to a culture may lead to the adoption of the stereotypes, animosities, and prejudices transmitted through the cultural environment, which may be acquired and expressed implicitly. Greenwald, McGhee, and Swartz (1998) demonstrated that Japanese American and Korean American students who had higher levels of familiarity with their native cultures exhibited stronger negative implicit attitudes, but not explicit attitudes, toward the other ethnic group. Among the most poignant examples of how the cultural milieu implicitly impacts the formation of prejudice is the tendency of ethnic minorities to exhibit positive implicit biases that favor the high-status majority group via unconsciously internalizing society's relatively negative evaluations of their own ethnic group (Dunham, Baron, & Banaji, 2008; Livingston, 2011).

Given the role that non-verbal learning and evaluative conditioning plays in the acquisition of intergroup bias, individual differences in intergroup bias may be partially shaped by an individual's sensitivity to evaluative conditioning. A study by Livingston and Drwecki (2007) revealed that variation in susceptibility to affective conditioning was a key psychological distinction between prejudiced and nonprejudiced individuals. Specifically, nonbiased individuals exhibited significantly weaker susceptibility to negative affective conditioning relative to biased individuals. These differences were observed using a domain-general affective conditioning task that used nonracial images as the conditioned (e.g., Chinese ideographs) and unconditioned (e.g., images of snakes, skulls, and spiders) stimuli. The findings suggest that generalized sensitivity to threat-based learning may be predictive of race-based intergroup bias. Social neuroscience has also contributed valuable neurobiological insights supporting the idea that out-groups may elicit aversive emotional responses such as fear or threat. Classic studies on intergroup perception in social neuroscience revealed that among White Americans, perceiving faces of Blacks relative to other Whites elicited activity within the amygdala, a neural structure involved in automatic processing of threatening and fear-relevant stimuli, as well as conditioned fear responses (Hart et al., 2000; LeDoux, 1996; Liddell et al., 2005; Öhman, 2005). Consistent with the notion that states of uncertainty and vigilance may provoke intergroup bias, the amygdala is also associated with alarm responses and processing ambiguous stimuli, which reflects more general functions in salience detection and processing motivationally relevant stimuli (Davis & Whalen, 2001; Whalen, 1998). Furthermore, amygdala reactivity to Black relative to White faces is also correlated with responses on automatic measures of racial bias (Phelps et al., 2000). Moreover, this heightened amygdala response to Black faces was also associated with startle responses (a measure of conditioned fear responses) to Black relative to White faces. Other studies have replicated the involvement of the amygdala in intergroup perception, as well as specifying the amygdala's role in relatively automatically processing of group membership (Cunningham et al., 2004) or when racial group membership is a salient processing goal (Wheeler & Fiske, 2005).

Similarly, regions involved in processing other negative affective responses may also play a role in the perception of out-group members. Negative evaluative conditioning may not be contingent on fear only. Readily associating disgust with potential contaminants and vectors for infection would have been an adaptive response, and it has been identified to contribute to the adoption of moral norms (Rozin & Fallon, 1987; Rozin, Haidt, & McCauley, 2008). The insula, a region that has been associated with processing visceral and social disgust (Craig, 2009; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003), as well as conditioning of disgust responses (Klucken et al., 2012), is recruited when perceiving members of stigmatized groups (Harris & Fiske, 2007; Krendl, Macrae, Kelley, Fugelsang, & Heatherton, 2006). Social neuroscience studies have also demonstrated that racial bias may be reflected neurobiologically through activity in regions associated with mechanisms to monitor, regulate, or suppress such negative evaluations or emotions toward out-group members, such as the dorsal–lateral prefrontal cortex (Cunningham et al., 2004; Richeson et al., 2003). Together, these findings suggest that one profile of neural activity when encountering or evaluating out-group members is represented by activity in regions associated with vigilance, processing threatening or aversive stimuli, or the regulation of such processes.

Thus far, there has been limited investigation in cultural neuroscience of the relationship between cultural norms that promote cohesion and cultural variations in systems involved in threat-based learning, such as evaluative conditioning. However, prior research has identified that individuals who report stronger support for policies perceived to protect the social unit (i.e., increased defense spending, harsher punishment for criminals, opposition to immigrants, and patriotism) exhibit increased levels of skin conductance arousal and startle eye blink response to threatening stimuli compared to those endorsing less support for such policies to protect the social unit (Oxley et al., 2008). Based on these findings, one promising avenue for future research may be investigating how the relationship between cultural systems promoting cohesion and intergroup bias is modulated by neurobiological mechanisms involved in threat-based learning. For instance, cultural environments that enforce strict and binding social norms may exert greater demands on heightened sensitivity of threat-based learning systems, which may indirectly lead to facilitated acquisition of intergroup bias through evaluative conditioning. Addressing such questions would be valuable not only for understanding cultural diversity in intergroup bias but also for providing insights into the mechanisms by which cultural transmission of intergroup bias occurs.

Some recent findings offer initial support for this relationship between exposure to threat, brain regions involved in learning and expressing threat-related responses, and cultural values that promote social cohesion and coordination (e.g., collectivism). A functional neuroimaging study by Chiao and colleagues (2015) suggests cultural variations in the responses of brain structures involved in processing threatening stimuli. In this study, Japanese and European American participants viewed aversive and threatening images (i.e., lunging snakes, skulls, and corpses) versus neutral images (configurations of shapes) while undergoing fMRI scanning. The authors observed that when viewing threatening relative to neutral images, greater responses were observed in both bilateral amygdala and bilateral insula among the Japanese relative to the American participants. Moreover, the authors examined the potential role of collectivistic values on modulating this group difference in neural responses in a follow-up study utilizing cultural priming of individualism/collectivism among Asian-American participants (Chiao et al., 2010). Compared to those primed with individualism, participants primed with collectivism exhibited greater responses in the bilateral amygdala to the threatening images. The authors proposed that sensitivity to negative information may be useful for achieving collectivistic cultural norms through advantages in detecting fear or disapproval from others. These recent studies lend support to our framework that cultural systems that promote social cohesion and neurobiological mechanisms involved in threat-related responses may mutually reinforce or bidirectionally shape one another (see Figure 17.1). Although we cannot directly infer that similar manipulations would also elicit stronger neural responses to stimuli reflecting out-groups associated with threat, behavioral studies have demonstrated that analogous cultural priming manipulations can induce more cooperation (vs. competition) toward in-group members relative to strangers (see Wong & Hong, 2005).

### *Genes Contributing to Threat Management*

Just as psychological and neurobiological responses associated with the processing and regulation of threat may correspond to both intergroup bias and cultural systems promoting social cohesion, genetic mechanisms that contribute to threat-relevant processes may also be predictive of intergroup attitudes and conduct. Prior research using twin studies has demonstrated that attitudes related to intergroup bias and discrimination (i.e., supporting statements such as "Black people are innately inferior to White people"), as well as support for policies that promote social order and security (i.e., support of extreme punishments for criminals), exhibit a significant degree of heritability (Bouchard et al., 2003; Lewis & Bates, 2010; Martin, Eaves, Heath, Jardine, Feingold, & Eysenck., 1986; Olson, Vernon, Harris, & Jang, 2001; Tesser, 1993). Yet despite the value of these twin studies that reveal the heritability of intergroup attitudes, it remains unknown what specific genes and associated polymorphisms may be contributing to intergroup bias. Given the critical role of threat in modulating intergroup bias and attending ideological attitudes, genetic polymorphisms that contribute to threat-relevant processing may serve as promising candidates.

One such candidate genetic mechanism is the functional polymorphism, *5-HTTLPR*, of the serotonin transporter gene (*SLC6A4*). This polymorphism is represented by two allele variants, short (S) or long (L), reflecting the length of the promoter region of *SLC6A4*, which influences the regulation of serotonergic neurotransmission. The less transcriptionally efficient S allele of the polymorphism is associated with higher concentrations of serotonin remaining in the synaptic cleft compared to the more efficient L allele, and this difference in the reuptake of serotonin has been associated with variations in affective processing based on genotype (Canli & Lesch, 2007). Behavioral genetics has implicated this polymorphism in a number of anxiety-, fear-, and threat-relevant outcomes. Specifically, those possessing at least one copy of the S allele (S/S and S/L) tend to exhibit a psychological phenotypic profile of heightened sensitivity and reactivity to threatening contexts and stimuli, evidenced by greater propensities for anxiety, vigilance, and risk aversion (Canli & Lesch, 2007; Caspi, Hariri, Holmes, Uher, & Moffitt, 2010; Crişan et al., 2009; Kuhnen & Chiao, 2009). Compared to those homozygous for the L allele, S-allele carriers also tend to exhibit greater discomfort with situations and decisions involving uncertainty or unfamiliarity (Chew, Ebstein, & Zhong, 2012; He et al., 2010). *5-HTTLPR* genotype has also been associated with threat-based learning mechanisms discussed previously, such that people who carry the S allele demonstrate heightened sensitivity to both personal and vicarious fear conditioning (Crişan et al., 2009; Lonsdorf et al., 2009), and they show greater reactivity to fear-relevant stimuli in the amygdala (Hariri et al., 2002; Munafò, Brown, & Hariri, 2008), a structure associated with evaluative conditioning and negative implicit racial biases (Cunningham et al., 2004; Öhman, 2005; Phelps et al., 2000).

Notably, many of the findings for complex social and psychological outcomes associated with *5-HTTLPR* have been based on gene × environment interactions. For instance, possessing the S allele of the polymorphism has been associated with personality traits, such as neuroticism and depressive/anxiety-related disorders, but only in conjunction with exposure to stressful, traumatic, or threatening events and experiences (see Caspi et al., 2010; Karg, Burmeister, Shedden, & Sen, 2011; Pluess, Belsky, Way, & Taylor, 2010; van Ijzendoorn, Belsky, & Bakermans-Kranenburg, 2012). Meta-analyses have indeed indicated that *5-HTTLPR* may moderate the relationship between stressful events and depression (Karg et al., 2011). Given the role that signals of potential out-group threat play in shaping intergroup bias, one plausible prediction is that *5-HTTLPR* may moderate the influence of such environmental signals of out-group threat on prejudice and in-group favoritism.

Cheon, Livingston, Hong, and Chiao (2014) sought to test this hypothesis. The authors observed patterns for gene × environment interactions on the acquisition of intergroup bias and prejudice among European American participants. In one study, participants reported their level of evaluative biases toward a number of out-groups that varied on stereotypicality of threat (e.g., Blacks, Arabs, Singaporeans, and people with schizophrenia). Participants also reported their level of prior negative interactions with members of each of these groups and completed the Belief in a Dangerous World Scale (BDW; Altemeyer, 1988) to assess how threatening personal experiences with these groups and general expectations of danger/exploitation by others may moderate intergroup bias. Consistent with the intergroup contact hypothesis (see Pettigrew & Tropp, 2006), the authors observed that participants who experienced relatively more negative prior contact with out-groups reported greater evaluative intergroup biases. However, this relationship was moderated by participant *5-HTTLPR* genotype, such that prior negative contact with an out-group was generally more strongly predictive of intergroup bias directed at the respective out-group among S-allele carriers relative to those possessing two L alleles.

The authors also observed an interaction between *5-HTTLPR* and BDW on intergroup bias. Prior research on the contribution of BDW to intergroup bias has suggested that such beliefs and expectancies about threat and exploitation from the social environment are especially predictive of stereotyping and biases against out-group members perceived to be threatening (Miller, Maner, & Becker, 2010; Schaller, Park, & Mueller, 2003). Accordingly, the interaction of BDW and genotype on intergroup biases was observed specifically for evaluations of out-groups the participants had rated to be the most threatening: Arabs and people with schizophrenia. The positive relationship between BDW and biases against these two stereotypically threatening groups was stronger among those who possessed the S allele of the polymorphism compared to those with two L alleles.

The authors followed-up these findings on the role of BDW with a minimal group paradigm that presented two ostensibly minimal out-groups that the participants played during the trust game (see Berg, Dickhaut, & McCabe, 1995). Members of one out-group played the game in a relatively untrustworthy manner, frequently betraying the participant, whereas members of the other out-group played in a relatively predictable and trustworthy manner. Through sampling the behaviors of out-group members during the trust game, participants were able to selectively associate one of the minimal out-groups with threat. To assess behavioral manifestations of intergroup bias (discrimination), participants were later asked to distribute raffles for prizes between a member of their minimal in-group and a completely novel member of the threatening and nonthreatening out-groups, who were not encountered during the trust game. Again, a *5-HTTLPR* × BDW interaction was observed for discriminatory raffle allocations selectively involving the threatening out-group member. The positive relationship between BDW and discriminatory allocations favoring an in-group member over a threatening out-group member was stronger among S-allele carriers relative to those with two L alleles. Because no prior stereotypes and prejudices exist for arbitrarily defined minimal groups, one implication of these findings is that *5-HTTLPR* may contribute to the *acquisition* of intergroup bias based on perceived threats from out-groups.

These findings suggest that in the presence of sufficient social experiences or expectations that facilitate the perception of out-groups as a source of threat, genetic polymorphisms that contribute to heightened sensitivity to the presence of threats may also be predictive of intergroup bias. Although understanding potential genetic contributions to intergroup bias is in nascent stages, these twin and candidate gene studies offer preliminary support for the notion that intergroup bias may be dually inherited and transmitted through the interplay of social (i.e., contextual cues of out-group threat) and biological mechanisms (i.e., genetic sensitivity toward threatening contexts) that regulate perceived intergroup threats.

Studies testing culture–gene coevolutionary theories (see Boyd & Richerson, 1985) by comparing national cultures and population frequencies of the S allele of *5*-HTTLPR have also suggested that *5-HTTLPR* may contribute to the adoption of cultural systems of sociality that promote cohesion, coordination, order, and structure. Given that diverse shared ecological threats may have promoted cultural systems of collectivism, tightness in norm enforcement, and hierarchical social organization (Gelfand et al., 2011; Murray & Schaller, 2010; Sidanius & Pratto, 1999), genotypes that may have conferred greater sensitivity and psychological reactivity to external pressures and threats may have served an adaptive function in such environments. Such biological dispositions could have facilitated the avoidance of potential fitness threats and the acquisition of cultural norms promoting conformity and cohesion.

Indeed, in cross-national analyses using national culture as a unit of analysis, cultures situated within regions facing greater intensity of historical environmental threats have been associated with greater endorsement of cohesive cultural values and practices. For instance, across regions of the world, historical prevalence of pathogenic threats has been positively associated with populations exhibiting greater *5-HTTLPR* S-allele frequencies and greater levels of collectivism (Chiao & Blizinsky, 2010). Similarly, Mrazek and colleagues (2015) have suggested that the relationship between diverse ecological threats and cultural tightness (vs. looseness) may be partially explained by greater S-allele frequencies among populations that faced greater historical ecological threats. Moreover, Fischer (2013) observed a gene × environment interaction on hierarchical cultural values such that regions that faced greater intensities of diverse environmental threats (e.g., food scarcity, territorial conflicts, and harsh climate) and consisted of higher population S-allele frequencies also exhibited greater levels of social hierarchy preferences.

One question is whether population frequencies of *5-HTTLPR* genotype and shared historical ecological threats may similarly be predictive of national indices of intergroup bias and discrimination. Noncontingent and overinclusive affiliation and trust toward others would lead to susceptibility and vulnerability to exploitation, infectious diseases, conquest by rivals, or suboptimal group cohesion (Axelrod & Hamilton, 1981; Brewer, 2004; Kurzban & Leary, 2001; Oaten et al., 2011). As such, parochialism or selectively prioritizing the welfare of in-group members may have been a characteristic of groups that were able to successfully navigate elevated uncertainties and threats from the environment. Those who may have been biologically predisposed to be more reactive to external threats may have also been more likely to engage in parochialism or in-group favoritism. Cheon and colleagues (2014) offer initial support for this view by demonstrating that perceptions of a dangerous world are more predictive of in-group favoritism in resource allocations among those possessing at least one S allele rather than two L alleles of *5-HTTLPR.* These findings at the individual level were further supported by analogous patterns among populations.

Using cross-national analyses, Cheon and Chiao (2012) observed that geopolitical regions with greater frequencies of the S allele of *5-HTTLPR* also exhibited greater national averages on measures of intergroup bias (e.g., favoritism for nationals vs. immigrants, nepotism, and mistrust of other nationalities). Furthermore, this relationship between S-allele frequency was contingent on the presence of ecological threats (e.g., pathogen prevalence and natural disasters), as well as cultural values for social hierarchy. When controlling for either external threat or cultural demands, which assumes equal levels of threats or cultural hierarchy values across regions, the relationship between regional S-allele frequency and intergroup bias was no longer significant. These cross-national comparisons recapitulate aspects of the gene × environment interaction findings from individual participants, suggesting that possessing at least one S allele may be predictive of intergroup bias in resource allocations only when individuals are exposed to signals of out-group threat (Cheon et al., 2014).

Further studies are necessary to test these culture–gene coevolutionary and gene × environment models of the interplay of perceived threats and *5-HTTLPR* on culture and intergroup bias. However, these initial studies offer promising insights into the role that genes associated with the processing and regulation of threat may play in the cultural diversity of intergroup dynamics. Although psychological outcomes associated with *5-HTTLPR* have been studied extensively in the social sciences, it is important to note that other functional genetic polymorphisms may also contribute to intra- and intergroup processes. Other candidates, including genetic polymorphisms that regulate dopaminergic neurotransmission (i.e., *DRD4*) and social bonding processes (i.e., *OXTR* and *AVPR1A*), may influence preferences for risk, reward, and social affiliation (see Kim et al., 2010; Kuhnen & Chiao, 2009), which may indirectly influence group processes.

### *Social Bonding/Affiliation in Response to Threats*

Although mechanisms that facilitate the detection and learning of threats are critical components of the psychological threat-management system, threats can also be regulated through bonding and affiliative responses. Likewise, psychological and neurobiological processes involved maintaining and bolstering affiliation may modulate intra- and intergroup conduct in response to threats. The need to affiliate with an in-group is inextricably linked to systems involved in threat management through attachment mechanisms (Ainsworth, 1982; Bowlby, 1988; Mikulincer & Shaver, 2007), which may extend to one's cultural group (Hong, Fang, Yang, & Phua, 2013). Consistent with human dependence on group living to survive and thrive (Brewer, 2004), in-groups satisfy a diverse array of fundamental needs, such as the need to belong and be socially accepted (Baumeister & Leary, 1995; Gardner, Pickett, & Brewer, 2000), epistemic needs that allow individuals to validate knowledge and reduce the experience of uncertainty (Hogg, 2007; Hogg & Abrams, 1993; Shah, Kruglanski, & Thompson, 1998; Webster et al., 1997), as well as enhancement needs that allow individuals to derive a sense of positive self-regard from the groups to which they belong (Aberson, Healy, & Romero, 2000; Rubin & Hewstone, 1998). As such, the disruption of fundamental psychological needs by perceived threats may motivate heightened in-group affiliation. The striving toward these fundamental psychological needs could consequently provoke stronger identification, cohesion, and affiliation with the in-group (Aberson, Healy, & Romero, 2000; Hogg, 2007; Noel, Wann, & Branscombe, 1995; Shah et al., 1998). Indirectly, heightened motivations for affiliation and bonding with the in-group may lead to parochialism, in-group favoritism, and the prioritization of the status and well-being of one's in-group, even in the absence of hostility, fear, or derogation of out-groups (Brewer, 1999; De Dreu, Greer, Van Kleef, Shalvi, & Handgraaf, 2011; Gaertner & Schopler, 1998).

As a result, intergroup bias may be reflected not only through patterns of neural reactivity in threat-relevant processing but also through selective responses of brain regions involved in social sensitivity and understanding, which may be necessary for facilitating identification, cohesiveness, and coordination among group members. When exposed to the suffering or needs of in-group and out-group members, the neural correlates of prosocial psychological processes such as empathy, mentalizing, and perspective taking are typically engaged to a greater extent toward in-group (vs. out-group) members (Cheon et al., 2011; Cikara, Botvinick, & Fiske, 2011; Mathur, Harada, Lipke, & Chiao, 2010; Xu, Zuo, Wang, & Han, 2009). However, this in-group favoritism in social sensitivity is not necessarily driven by indifference to the suffering of out-group members. Although the suffering of others may provoke heightened empathic responses regardless of their group membership, the suffering of in-group members may elicit especially elevated empathic responses, or "extraordinary empathy" (see Mathur et al., 2010), over and above the empathy experienced for out-group members. This finding supports the idea that intergroup bias need not be dependent on out-group hostility, and in-group favoritism can be observed even in contexts that increase generalized sensitivity to others (including out-group members). Similarly, the intranasal administration of the neuropeptide oxytocin, which is involved in affiliative and bonding behavior (Bartz, Zaki, Bolger, & Ochsner, 2011; Campbell, 2010), has been identified to heighten in-group favoritism, parochialism, and defensiveness of in-group members (De Dreu et al., 2010, 2011; Sheng, Liu, Zhou, Zhou, & Han, 2013). Furthermore, this in-group positivity associated with oxytocin was observed even in the absence of heightened negativity or derogation directed at out-groups.

Thus, future studies examining the role of threat on intergroup processes and cohesive cultural practices may benefit from not only focusing exclusively on neurobiological systems involved in detecting and encoding threat but also focusing on parallel systems involved in modulating social affiliation and attachment responses.

## Implications for Health-Related Outcomes

A cultural neuroscience framework for understanding the relationship between threat and intergroup processes may also contribute insights into the relationship between group processes and health. Diathesis-stress models have consistently revealed the critical role that the exposure to stressors and threats may play on health and well-being, especially among those who are biologically predisposed to vulnerability to threats (Belsky & Pluess, 2009; Caspi et al., 2010). Prior research has suggested that living in fear of exploitation and harm from others can be a risk to well-being, as well as physical and mental health (Ranjit et al., 2007; Ross, 1993; Stafford, Chandola, & Marmot, 2007). In a diverse society in which common external threats (i.e., economic troubles, crime, scarcity of resources, and diseases) may be attributed to out-group members, heightened levels of distrust, anxiety, and fear from out-groups may lead to exacerbated risks to health and psychological well-being among the public.

Although threats and fears of being harmed, harassed, or exploited by others may be one source of social stress, self-threats associated with being rejected or subjected to negative evaluations may have profound and lasting influences on physiological stress and the immune system (Dickerson, Gruenwald, & Kemeny, 2004; Dickerson & Kemeny, 2004). Research by Trawalter, Adam, Chase-Lansdale, and Richeson (2012) demonstrated that anxiety and vigilance about being perceived negatively during interracial contact can mobilize physiological stress responses. Participants engaged in a video-recorded interracial or non-interracial interaction and provided salivary cortisol samples before and after the interaction. Analysis of stress- and threat-related spontaneous postures and behaviors of participants in the recordings (e.g., averted eye gaze, rigidity, and lower amounts of smiling) revealed that participants who endorsed greater concerns about appearing prejudiced exhibited more stress-related postures and gestures during the interracial interaction. Similarly, participants expressing more anxieties about appearing prejudiced also exhibited heightened levels of cortisol stress responses during the interracial contact. Moreover, the authors also observed that chronic and recurring situations of interracial contact coupled with higher worries about appearing prejudiced may lead to chronic changes in the cortisol stress response system. Participants (freshman university students) in a follow-up study provided regular diary entries regarding their most meaningful interactions with others from the fall to the spring sessions of an academic year. Among those who reported greater levels of meaningful interracial contact over this period, maintaining higher concerns about appearing prejudiced was associated with flatter diurnal cortisol slopes (an indicator of chronic stress) during the spring compared to the fall of the academic year. These findings suggest that chronic anxieties experienced during interracial contact may predict changes in the physiological stress system over time.

Heightened anxiety, uncertainty, and vigilance associated with concerns of being negatively evaluated or discriminated in interracial contexts can have negative downstream consequences on diverse health outcomes. Perceived or anticipated discrimination has been associated with exacerbated stress responses, compromised mental and cardiovascular health, greater risk of alcohol and drug abuse, and lower levels of seeking and complying with health services (Sawyer, Major, Casad, Townsend, & Mendes, 2012; for review, see Williams & Mohammed, 2009). Among older adults, perceived discrimination also contributes to higher risk of mortality (Barnes et al., 2008). Notably, discrimination was measured with items that included reflections of how often others threatened or treated the respondent as a potential source of threat (e.g., act as if you are dishonest, act as if they are afraid of you, and threaten and harass you). Together, these findings suggest that heightened vigilance or perceived threats to the self in the context of recurring interracial interactions may have long-term detrimental consequences on health and well-being.

Moreover, such negative consequences of heightened perception of out-group threat and expected self-threats in interracial interactions may be exacerbated among those who may have elevated biological sensitivities to threat. For instance, those possessing two S alleles of *5-HTTLPR* were identified to exhibit greater cortisol stress responses following a social stressor signaling potential negative evaluations and disapproval by others (Way & Taylor, 2010). Similarly, using fMRI, Ma and colleagues (2013) observed that those possessing S/S genotypes (compared to L/L genotypes) of *5-HTTLPR* reported greater distress and exhibited stronger responses in the anterior insula, anterior cingulate cortex, and medial prefrontal cortex when reflecting on negative qualities of the self. These findings were not in an interracial or intergroup context. However, when taken into consideration in conjunction with the results of Trawalter and colleagues (2012) on physiological stress responses to negative self-evaluation in interracial contexts, these studies suggest that individual differences in neurobiological systems of threat management may also modulate the relationship between interracial relations and outcomes pertaining to stress and well-being. Future investigations into the role of biological and social threat-management systems in the cultural neuroscience of intergroup relations may be promising for clarifying how systematic intergroup discrimination and rejection may translate into health disparities.

## Threats as Opportunities for Intergroup Cohesion and Cooperation

Throughout this chapter, we have explored the cultural, psychological, and neurobiological mechanisms by which threats indirectly produce intergroup bias. But are intergroup relations always doomed to break down in the face of external threats?

Our view is that external threat is not always deterministic of intergroup bias—especially when external threats are shared between groups. Threats exert pressures toward cohesion; thus, shared threats between groups may provide a powerful opportunity for fostering intergroup cohesion and cooperation. The common in-group identity model (Gaertner, Dovidio, Anastasio, Bachman, & Rust, 1993) proposes that one mechanism for prejudice reduction involves the psychological recategorizing of in-group and out-group members into a common and inclusive superordinate group. This recategorization is facilitated by superordinate goals that foster cooperation. Notably, the adoption of a common in-group identity that is inclusive of former out-group members may reduce intergroup bias by decreasing perceived threats from the out-group (Hong et al., 2004; Riek et al., 2006). Similarly, theories of prejudice reduction through intergroup contact propose that intergroup contact may be optimally effective under cooperative contexts (Allport, 1954; Pettigrew & Tropp, 2006). In the Robber's Cave experiment (Sherif, 1961), efforts to integrate two competitive and hostile groups of boys at a summer camp were less effective when they simply involved shared activities (e.g., watching a film or eating together). Instead, positive intergroup relations were forged when the groups were required to overcome a shared threat, such as repairing a malfunctioning supply of drinking water.

Thus, collectively shared threats may serve as a basis for intergroup cooperation rather than division. In these contexts, the sensitivity and reactivity of psychological/neurobiological systems associated with threat management may be associated with *heightened* intergroup cooperation and prosociality. For instance, greater sensitivity and reactivity to threats may facilitate the adoption of a superordinate in-group identity or efforts to establish cooperation and coordination with out-groups that share the same threat. Although possessing at least one S allele of *5-HTTLPR* was predictive of greater intergroup bias compared to those with two L alleles when exposed to more negative experiences of intergroup contact (Cheon et al., 2014), the authors also observed a reversal of this relationship among those who reported relatively more positive experiences of intergroup contact. When participants reported relatively more positive past experiences with out-groups (suggesting more cooperative intergroup relationships), those who possessed at least one S allele of *5-HTTLPR* (compared to two L alleles) exhibited tendencies toward *lower* intergroup bias. These findings indicate that biological systems involved in detecting and regulating threats may contribute to the plasticity of intergroup bias to contextual intergroup demands rather than predicting intergroup bias in a static, inflexible, and unidirectional manner.

Despite the potential positive effects that shared threats may have for forging intergroup cooperation, threatening contexts may also present hindrances to common in-group identity formation. When faced with a looming threat, concern for in-group members may lead to the misattribution or underestimation of the extent to which the threat also affects out-groups. Even worse, given the tendency for threatening cues to be readily conditioned to representations of out-group members (Navarette, et al., 2009; Olsson et al., 2005), threats may be attributed to or blamed on the out-group (see Douglas, 1992), even though the out-group is subjected to the same threats. Furthermore, superordinate categories that are assumed or associated more readily with the in-group may counterproductively lead to the exclusion of out-groups. For instance, the label "American" is stereotypically associated with White Americans (Devos & Banaji, 2005). Consequently, recategorizing White American participants into the superordinate group "Americans" produced greater blame for the devastation of Hurricane Katrina on the predominantly African American victims and lower blame attributed to racism (Dach-Gruschow & Hong, 2006). Considering these potential boundary conditions to the benefits of common in-group identities, future research that identifies optimal conditions for fostering intergroup cooperation in the face of shared threats will be especially promising.

## Conclusion

Culture serves adaptive functions for resolving challenges associated with the ecology and group living. Accordingly, culturally modulated processes such as intergroup bias are also situated within a system consisting of ecology, local means of social organization and structure, and the modulating influence of these physical/social environments on the mind and brain. Ever more diversifying, globalizing, and multicultural societies offer exciting opportunities for creativity, innovation, and progress but also pose challenges for averting parochialism and group insularity. Through synthesizing the ecological, social, psychological, and neurobiological systems that underlie intra- and intergroup dynamics, the cultural neuroscience of intergroup processes offers promise as a critical field of study for understanding how we can promote constructive and healthy relations in our ever-diversifying social world.

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## CHAPTER 18

# Cultural Neuroscience of Pain and Empathy

Joan Y. Chiao *and* Vani A. Mathur

**Abstract**

Population health disparities exist in the prevalence of pain throughout the world due to social and biological factors. We examine the etiology of population health disparities in pain prevalence with the cultural neuroscience model. We review empirical evidence for population health disparities in acute and chronic pain, particularly in people from the United States of different racial and ethnic heritages. We discuss how culture, race, and ethnicity affect pain and empathy at the level of neurobiology as well as how an understanding of the mechanisms underlying population health disparities in pain can lead to more effective treatments in multicultural and cross-cultural communities. Implications for understanding the etiology of pain prevalence from a cultural neuroscience perspective for public health are discussed.

**Key Words:** cultural neuroscience, pain, empathy, population health disparities, etiology

## Population Health Disparities in Pain

The World Health Organization reports that persistent pain is one of the most prevalent medical conditions throughout the world (Green et al., 2003; Gureje, Von Korff, Simon, & Gater, 1998). Approximately 5.5–33% of primary care patients report experiencing persistent pain for more than 6 months. People who suffer from persistent pain are more likely to experience less psychological well-being, lower physical well-being, as well as be perceived by physicians as experiencing worse health status (Gureje et al., 1998). In the United States alone, chronic pain costs approximately $635 million annually in treatment as well as lost productivity (Institute of Medicine, 2011). Within- and cross-national differences in pain prevalence indicate population health disparities in pain experience and treatment.

In this chapter, we explore the etiology of population health disparities in pain from a cultural neuroscience perspective by (1) discussing how to study population health disparities with a cultural neuroscience model; (2) reviewing empirical evidence for population health disparities in acute and chronic pain, particularly in people from the United States of different racial and ethnic heritages; (3) reviewing empirical evidence for cultural, racial, and ethnic differences in the neurobiology of pain; and (4) examining how population health disparities in pain arise due to cultural, racial, and ethnic factors and the implications of these theories and findings for pain treatment within and across multicultural and monocultural communities.

## Understanding Population Health Disparities: A Cultural Neuroscience Model

Population health disparities refer to differences in health outcomes or disease prevalence across groups due to reasons that are unjust or unfair. Both sociocultural and biological factors may play a role in population health disparities related to pain and empathy. Sociocultural factors, such as culture, race, and ethnicity, have been shown to contribute to differences in chronic and acute pain prevalence and treatment across multicultural and monocultural communities (Gureje et al., 1998; Rahim-Williams, Riley, Williams, & Fillingim, 2012). Biological factors may also contribute to population differences in pain prevalence, including genetic variation in pain across racial or ethnic groups (Kim et al., 2004), gene × environment factors of pain experience (Nielsen et al., 2008) that differ across racial or ethnic groups, as well as culture × gene × environment interactions that contribute to pain perception and experience.

Cultural neuroscience is a field that examines how cultural values, practices, and beliefs affect biological processes in the production of human behavior (Chiao & Ambady, 2007; Chiao, Cheon, Pornpattananangkul, Mrazek, & Blizinsky, 2013; Cheon, Mrazek, et al., 2013). A majority of behavioral and neuroscience research has been conducted primarily in Western, educated, industrialized, rich, democratic (WEIRD) populations (Chiao, 2009; Henrich, Heine, & Norenzayan, 2010), indicating that a complete understanding of the etiology of pain may be impoverished by the lack of scientific behavioral and neuroscience investigation of pain in culturally diverse or cross-cultural communities. Findings in cultural neuroscience may contribute to a better understanding of population health disparities by identifying key sociocultural and biological factors that cause mental and physical health outcomes across diverse populations (Chiao & Blizinsky, 2013), such as those that are associated with feelings or experience of pain. Researchers in cultural neuroscience rely on multiple noninvasive methods to examine how culture affects neurobiological processes. One of the challenges with studying chronic and acute pain with a cultural neuroscience approach is ensuring cross-site and cross-cultural validation of pain assessment. Given the subjectivity in the experience of pain (Mathur, 2012) as well as the known response biases that vary across races and ethnicities, it is important to consider the utility of nonverbal, noninvasive measures of pain experience, such as biomarkers.

One proposed biomarker of pain in humans is a neural signature or network of pain-related brain regions measured with functional magnetic resonance imaging (fMRI), specifically including the ventrolateral thalamus, secondary somatosensory cortex, dorsal posterior insula, anterior insula, and anterior cingulate cortex (Wager et al., 2013). Recent advances in pain neuroimaging show that nonclinical physical pain can be specified within neural signatures measured by fMRI with approximately 70–95% or more sensitivity depending on the type of physical pain stimulus (Wager et al., 2013). However, little is known about how neural biomarkers of pain may vary as a function of culture, race, and ethnicity, as well as how neural biomarkers may inform closing the gap in population health disparities of pain. In the next section, we briefly review behavioral studies that demonstrate population health disparities in pain experience.

## Culture, Race, Ethnicity, and Pain

Nearly two decades of behavioral research on pain disparities shows that the subjective experience of pain is affected by a person's culture, race, and ethnicity. Meta-analytic evidence demonstrates that African Americans typically show lower physical pain tolerance compared to non-Hispanic Whites, likely due to both sociocultural and biological factors (Rahim-Williams et al., 2012). In experimental studies, African Americans are more likely to show lower physical pain thresholds to different types of physical pain stimuli, including cold, heat, pressure, and ischemic pain (Rahim-Williams et al., 2012). Acculturation likely also plays an important role in physical pain sensitivity (Chan, Hamamura, & Janschewitz, 2013). Chan and colleagues (2013) showed heightened pain responses for mainland Chinese students compared to Hong Kong Chinese students as well as in first-generation Asian Americans compared to first-generation Caucasian Americans and second-generation Caucasian Americans and Asian Americans.

One possible explanation for this racial disparity in physical pain experience is the presence of historical and contemporary social pressures, such as racial discrimination. Racial minorities in the United States, African Americans and Hispanics, have faced distinct kinds of social pressures, such as discrimination and marginalization. In order to cope with these social pressures, cultural customs or values shared within the group may be created and sustained within the group. Ethnic identity, for instance, refers to the extent to which people identify with their ethnic group with knowledge of the values and customs typically observed within the group (Phinney, 1990). Prior behavioral research has shown that African Americans and Hispanics who reported stronger identification with their ethnic group also showed enhanced sensitivity to pain (Rahim-Williams et al., 2007). African Americans also report greater levels of catastrophizing and passive coping that has already been shown to lead to greater sensitivity in pain (Rahim-Williams et al., 2007). Despite convergent behavioral evidence that racial disparities in pain perception and experience exist within the United States, particularly for African Americans and Hispanics, little is known about the specific biological mechanisms that cause racial disparities in pain as well as how such disparities may be treated with pharmacological or cultural interventions. In the next section, we discuss recent cultural neuroscience evidence that begins to identify key neural circuitry of pain and empathy modulated by culture, race, and ethnicity.

## Cultural Neuroscience of Pain and Empathy

Research in cultural neuroscience shows that culture, race, and ethnicity affect neurobiological bases of pain and empathy (Chiao & Mathur, 2010; Chiao, 2011). Cultural group membership has been shown to affect the extent to which neural response within anterior cingulate cortex (ACC) is heightened during perception of physical pain in others in Chinese and Europeans living in China (Xu, Zuo, Wang, & Han, 2009). These findings indicate that brain regions such as the ACC show varying levels of recruitment depending on physical characteristics of the expresser, specifically the race or ethnicity of the person expressing pain or suffering to another. Conceptual characteristics, such as cultural values of hierarchy preference or social dominance orientation (SDO), have also been shown to modulate neural responses when people empathize with emotional pain expressed by group members in South Korea and the United States. Cheon and colleagues (2011) found that for Koreans and Caucasian Americans, SDO predicts empathy for group members and neural response within the left temporoparietal junction mediates the relation between cultural values of hierarchy and intergroup empathy. Furthermore, Cheon, Im, and colleagues (2013) showed that collectivistic values, such as other-focusedness or a belief that the success or failure of others is important to one's own self, is correlated with empathic neural response within ACC and insula for Koreans but not for Caucasian Americans.

For people living in social environments with social or political pressures to either maintain or ameliorate intergroup conflict, the ability to feel the pain or suffering of others who are not group members may be affected in different ways. Arabs and Israelis who recently immigrated to the United States showed reduced empathic neural response to narrative descriptions of the pain and suffering of out-group members of the conflict group but not for South Americans (Bruneau, Dufour, & Saxe, 2012). These findings support the notion that learning about the pain and suffering from others does not elicit a neurobiological response consistent with that of others who are within their group. Similarly, regulation of empathy for aggressive emotions, such as anger, is an important social adaptation for maintaining cultural norms that emphasize social harmony and interdependence, thereby reducing social pressures and potential for intergroup conflict. A recent transcultural neuroimaging study of Germans and Chinese found greater response within the left dorsolateral prefrontal cortex during empathy for anger for Chinese, suggesting that neural mechanisms of self-regulation are recruited to a greater extent during empathy for negative emotions in order to facilitate interdependence and social harmony within the group (de Greck et al., 2012). Cultural values likely require the sustained recruitment of distinct neural circuitry when people feel others' negative emotions, such as pain and anger.

Race and ethnicity have also been shown to modulate neurobiological mechanisms of empathy. African Americans and Caucasian Americans show increased neural response within the medial prefrontal cortex when empathizing with emotional pain and suffering of others within their social group caused by environmental pressures, such as a natural disaster (Mathur, Harada, Lipke, & Chiao, 2010). Furthermore, Mathur, Harada, and Chiao (2012) found that people with higher ethnic identification, such as African Americans, show increased response midline regions during empathy for group members compared to Caucasian Americans, who show lower ethnic identification and increased response within parahippocampal regions. These findings indicate that the degree to which a person thinks and identifies with people who share the same group membership, including customs, beliefs, and practices, affects which neural systems are recruited when feeling the pain or suffering of others within their group.

The experience of social pain may be enhanced or ameliorated depending on the extent of racial prejudice and discrimination within the social environment. For African Americans, experiencing social pain due to social exclusion from Caucasian Americans may lead to reduced neural response within social pain regions compared to when they experience social pain when the social exclusion is attributable to racial discrimination or group-based exclusion rather than person-based exclusion (Masten, Telzer, & Eisenberger, 2011). For both Whites and Blacks living in Europe, negative implicit racial bias predicts increased neural response within the left anterior insula during the observation of physical pain in one's own group members (Azevedo et al., 2013). Unconscious racial attitudes or biases that facilitate social inclusion for in-group members and social pain for out-group members affect the degree to which people demonstrate empathic neural response to even the physical pain of others.

## Implications for Pain Treatment and Future Research

Treatment for numerous chronic diseases and acute physical injuries involves identifying effective methods for ameliorating patient pain. The extent to which pain treatment is successful may be affected by both sociocultural and biological factors associated with the extent to which a physician or healthcare worker within a medical setting can empathize or sympathize with the pain and suffering of the patient. Minorities within the United States, such as African Americans and Hispanics, are less likely to receive pain treatment (Anderson, Green, & Payne, 2009), despite heightened exposure to social or environmental pressures that can cause pain or injury. Cultural values or beliefs of minority Americans may lead to a mistrust of medical treatment by medical care professionals in cross-race medical settings.

Social factors, such as unconscious racial prejudice and social status, affect the extent to which people perceive pain treatment as appropriate for minorities. Trawalter, Hoffman, and Waytz (2012) showed that people perceive Black athletes (e.g., football players) as less likely to feel physical injuries compared to White athletes due to social status or perceived hardship. Relatedly, physicians were more likely to prescribe opioids for physical pain of the patient with a prestigious occupation (Tamayo-Sarver et al., 2003). Drwecki, Moore, Ward, and Prkachin(2011) found that when nursing professionals were asked to recommend the best medical care to Whites and Blacks displaying genuine facial expressions of pain, positive racial biases for Whites predicted heighted quality in pain treatment. Notably, Mathur and colleagues (2013) showed that when race of a patient is made consciously salient, biases in recommendations for pain treatment are reduced. Understanding the role of unconscious and conscious prejudice as well as socioeconomic status (Poleshuck & Green, 2008) in pain experience and treatment remains a priority in closing the gap in pain disparities. Future research in cultural neuroscience has the potential to provide a critical foundation for pain diagnosis and treatment for people, regardless of culture, race, or ethnicity. By discovering how and why pain disparities exist, we come close to achieving fair and equitable health care for all.

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# PART 6

# Culture and Genetics

CHAPTER

19

# The Gene–Culture Interaction Framework and Implications for Health

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## Abstract

Based on the framework of gene–environment interactions (G × E), the gene–culture interaction framework demonstrates that a more complete understanding of thoughts and behaviors relevant to health may come from incorporating both genetic and cultural factors. Genes may interact with culture such that genetic predispositions lead to different outcomes depending on culture, and cultural differences on a given outcome may vary depending on genetic predispositions. We provide an overview of G × E research and some of the underlying biological mechanisms of these interactions. We explain the gene–culture interaction framework and discuss how culture is an important form of environment to consider that makes theoretical contributions unique from other forms of environment typically studied in G × E research. We discuss theoretical questions raised by gene–culture interaction research and specify how the gene–culture interaction framework can be applied to certain health issues.

**Key Words:** gene–environment interaction, gene–culture interaction, determinants of health, framework, culture

Imagine two wine grape varieties across two different climates. Whereas the Cabernet Sauvignon variety may thrive in warm climates, the ideal climate for Riesling is relatively cooler. Knowing when and why grapes produce optimal fruit for good wine requires understanding the *interaction* of a number of factors, such as grape variety based on genes and climatic aspects of the environment: These grape varieties thrive in either warm or cool climates, depending on their particular variety. Similarly, variation in human thought and behavior relies on both genetic and environmental factors, as well as the interaction between the two. Focusing only on genetics as a source of variation ignores the reality that the same genetic tendency can lead to different outcomes according to the environment. Likewise, focusing on the environment as the sole explanatory force overlooks the fact that the same environment can have different consequences for people depending on their genetic tendencies. In order to make predictions about when or why people think and behave the way they do, it is useful to consider their biological predispositions together with the particular environmental context in which they exist.

Among the many ways in which environments vary, culture—the part of the environment created and shared among social beings and passed down over generations (de Waal, 2001; Geertz, 1973; Herskovits, 1948; Triandis, 2007)—is one important aspect of environmental variation that has only recently been considered together with genes. Cultural psychology is a field that investigates cultural variation in systematic ways and has grown considerably in its breadth of topics and scientific approaches during the past 25 years. Recently, the emerging field of cultural neuroscience has built on cultural psychology, tackling questions on culture, mind, and the brain by integrating cultural psychological research with cutting-edge techniques and perspectives from neuroscience (for review and proposed framework of cultural neuroscience, see Kim & Sasaki, 2014). Using cultural psychology and cultural neuroscience as foundations, our research has examined gene–culture interactions, or the dynamic interplay of genes and culture as they jointly influence psychological outcomes (Kim, Sherman, Sasaki, et al., 2010; Kim, Sherman, Taylor, et al., 2010; Kim et al., 2011). Our perspective is that not only do both genes and culture act as independent sources of influence but also, importantly, they interact to predict various outcomes. Therefore, the gene–culture interaction framework examines how culture can shape the way genetic tendencies are expressed and also how cultural influences may change depending on genetic predispositions.

Because the gene–culture interaction framework considers the sociocultural context as one source of psychological variation that interacts with biological predispositions, this framework may be important for understanding the complexities surrounding health within and across diverse societies. In particular, many issues relevant to physical and psychological health, including the determinants of health outcomes, treatments for health problems, and intervention strategies, may vary across cultures. Within any society, there exist groups of people that differ along multiple dimensions. In addition to ethnicity or nationality, which are the most commonly studied dimensions of culture, there are many other forms of culture (Cohen, 2009) that have important health implications, such as religion (Koenig & Larson, 2001; McCullough, Hoyt, Larson, Koenig, & Thoresen, 2000), region (Plaut, Markus, & Lachman, 2002), and social class (Adler, Epel, Castellazzo, & Ickovics, 2000; Adler & Stewart, 2010; Plaut, Markus, Treadway, & Fu, 2012). These different forms of culture vary not only within but also across societies, and therefore, using a cultural perspective can help broaden understandings of health beyond the populations that tend to be studied most (i.e., "WEIRD" participants who are *W*estern, *e*ducated, *i*ndustrialized, *r*ich, and *d*emocratic; Henrich, Heine, & Norenzayan, 2010a, 2010b). At the same time, there are important individual differences in genetic predispositions, and these predispositions may predict health outcomes differently depending on the cultural context. Given that genes interact with environmental factors to influence health-related outcomes (e.g., Caspi et al., 2003; Johnson & Krueger, 2005; Kim-Cohen et al., 2006; Larsen et al., 2010; Miller et al., 2009; Schmid et al., 2010; Taylor et al., 2006) and that there are cultural differences in how people strive for and achieve a healthful life (Oishi & Diener, 2001; Plaut et al., 2012), the gene–culture interaction framework has great potential for predicting and explaining the complexity that surrounds health issues for diverse groups.

In this chapter, we first provide an overview of research on gene–environment interactions (gene × environment, or G × E) and the biological mechanisms underlying these interactions. Second, we explain the framework of gene–culture interactions (gene × culture, or G × C), including how this framework builds on gene–environment research and makes unique theoretical contributions. We also discuss some potential mechanisms of gene–culture interactions, review empirical evidence supporting the G × C framework, and bridge the framework with a prominent theory in the study of genes and culture—that of gene–culture coevolution. In the next section, we discuss theoretical issues and questions raised by G × C research, including implications for findings in cultural psychology and issues surrounding covariation of cultural and genetic differences. Finally, we specify how the G × C framework can be applied to health research. In so doing, we explain the theoretical value of taking a cultural perspective in issues of health, suggest future areas of research relevant to health, and offer insight on how this research has implications for public health policy.

## Gene–Environment Interactions and Underlying Biological Mechanisms

The framework of gene–environment interactions (G × E) is one that should seem familiar to many psychologists, particularly in social and personality disciplines, and it also has certain advantages compared to other interactionist models of behavior. The idea that something about the person (in this case, genes) interacts with something in the environment (e.g., the social context) is reminiscent of classic work from person × situation theory (Mischel, 1990; Mischel & Shoda, 1995), which addresses how personality can interact with situational contexts to influence behavior. Consideration of genetics from a similar perspective raises a number of novel questions and potential implications for psychology. Some of the underlying biological mechanisms of G × E interactions, for example, may potentially be incorporated into theories of psychological phenomena. Genetics research also offers a particularly promising way to contribute to an understanding of cultural differences in basic psychological processes, including health-related outcomes.

The long-standing nature–nurture debate focuses on distinguishing the distinct influences of genes versus environment. Rather than treating the two factors separately, the G × E interaction framework describes the phenotypic effects of interactions between individual genetic variation and the environment. The framework proposes that environmental conditions may moderate the psychological outcome of a particular genetic sequence or that genetic predispositions may moderate the relationship between the environment and an outcome (Caspi et al., 2002, 2003). In other words, an individual could be genetically predisposed toward a particular psychological outcome, but that outcome may only occur given specific environmental pressures. For example, Caspi and colleagues (2003) found that carrying the short (s) allele of the *5-HTTLPR* polymorphism of the serotonin transporter (*SLC6A4*) gene promoter region increases the likelihood of showing depressive symptoms compared to carrying the long (l) allele, but only when coupled with exposure to life stress (for recent meta-analytic support of this G × E finding, see Karg, Burmeister, Shedden, & Sen, 2011; but see also Risch et al., 2009).

Originally studied in the context of disease susceptibility, genes implicated in environmental sensitivity, such as the s allele of *5-HTTLPR*, have been referred to as "risk" genes (e.g., Caspi et al., 2003). Recently, however, such genes have been reconceptualized as "plasticity" genes, rather than as linked to mostly positive or mostly negative outcomes, in order to highlight the malleability rather than valence of particular genetic predispositions (Belsky et al., 2009). In addition to *5-HTTLPR* (Caspi et al., 2003; Cheon, Livingston, Hong, & Chiao, 2014; see also Chapter 17, this volume), G × E interactions have been reported for various other genes, including the gene encoding monoamine oxidase A (*MAOA*) (Caspi et al., 2002; Foley et al., 2004; Kim-Cohen et al., 2006) and the dopamine D4 receptor (*DRD4*) gene (Bakermans-Kranenburg & van IJzendoorn, 2011; Sasaki et al., 2013). In a study of intervention effects on child behavior, a repeat polymorphism in *DRD4* moderated the effectiveness of the intervention (Bakermans-Kranenburg & van IJzendoorn, 2011), suggesting a differential susceptibility to environment inputs dependent on genetic differences. Another study investigating the interaction between the environment and variants of the *DRD4* gene found G × E interactions on even short-term exposure to environmental conditions: Participants carrying 2- or 7-repeat allele variants of *DRD4* were more susceptible to the influence of religion priming on prosocial behavior compared to participants without these variants (Sasaki et al., 2013). Across multiple genes and investigations, there is evidence that people with certain genetic variants of "plasticity genes" may be more susceptible to environmental influence in particular domains.

At the molecular level, environmental factors may interact with genes by influencing the regulation of gene expression, which is a crucial link between genes and their phenotypes. Gene expression is the process of synthesizing a biologically functional molecule from DNA, and the capacity to adapt gene expression in response to physiological changes or environmental conditions is a basic biological mechanism. For instance, in response to being wounded, an injured organism might upregulate the expression of genes relevant to wound recovery (Slavich & Cole, 2013). Similarly, external social factors could activate biological pathways to regulate gene expression. Stress and social isolation, for instance, have long been associated with poorer immune system functioning (Seeman, 1996), and a study examining white blood cells provided evidence linking social to biological factors at the level of gene expression (Cole et al., 2007). In particular, among adults who felt less socially connected, pro-inflammatory genes were upregulated, whereas anti-inflammatory genes were downregulated, providing molecular evidence for the relation between social isolation and elevated risk for inflammatory disease.

Social signal transduction, first studied in the context of animal models (Robinson, Ferald, & Clayton, 2008), is a process explaining how social conditions might alter gene expression through transcription factors, which are proteins that regulate the transcription of DNA into mRNA (Slavich & Cole, 2013). Specifically, social signal transduction emphasizes that subjectively perceived social environment threats may affect hormone and transmitter levels, leading to changes in the activity of transcription factors. For instance, feelings of loneliness or social isolation have been linked to the activation of inflammatory genes and inhibition of antiviral genes (Slavich et al., 2010), and even the mere threat of social loss appears sufficient to alter gene transcription dynamics (Miller et al., 2008). The process of social signal transduction underscores the point that an individual's subjective perception of social conditions as either threatening or nonthreatening may at times be more influential than what is objectively the case (see also Chapter 17, this volume).

Individuals may also vary in their signal-transducing potential depending on differences in their genes. For example, a study on the link between environmental adversity and health outcomes examined a single nucleotide polymorphism (SNP) in the promoter region of the human interleukin-6 (IL-6) gene, which is involved in the inflammatory response (Cole et al., 2010). Particularly within the promoter and enhancer region of genes, genetic sequence variations such as SNPs may alter the binding affinity of transcription factors. This SNP of IL-6 inhibits binding of the transcription factor *GATA1*, which typically activates in response to environmental adversity, and thus, people carrying the low-binding-affinity variant of the IL-6 gene show an inflammatory response that is unrelated to exposure to environmental adversity.

Behavioral and health outcomes may also be influenced by epigenetics, which are processes that can affect gene expression without altering the underlying genetic sequence (Ledón-Rettig & Pfennig, 2012). Molecular-level processes, such as methylation, or the addition of methyl groups, may prevent transcription factors from accessing DNA, possibly preventing the synthesis of gene products. A key finding on how epigenetic processes contribute to behavioral variation showed that maternal care in rats is associated with differential methylation of the glucocorticoid receptor (GR) promoter region in the brain hippocampi (Weaver et al., 2004, 2005). The offspring of rat mothers who naturally exhibited greater pup licking and grooming behavior showed decreased methylation of the GR promoter region in the hippocampi. Greater methylation of the GR promoter has been found to reduce gene expression and to lead to a greater disposition for anxiety (Meaney, 2001; Weaver et al., 2004).

In humans, there is evidence that epigenetic regulation of genes may be involved in various social processes and mental health outcomes. For example, in a study investigating methylation status of a regulator region (CpG island) of the oxytocin receptor gene (*OXTR*) in peripheral blood cells and temporal cortex, individuals with autism showed increases in methylation compared to controls (Gregory et al., 2009). The increased methylation of this regulator region was specifically associated with decreased *OXTR* transcription in an area of the temporal cortex adjacent to the temporal parietal cortex and near the superior temporal sulcus (STS), a brain region implicated in social cognition (Allison, Puce, & McCarthy, 2000; Pelphrey & Morris, 2006). DNA methylation of *OXTR* may also play a role in individual variation in social information processing. The DNA methylation status of *OXTR* was found to predict neural activation of areas of the brain implicated in social processing in response to ambiguous social stimuli (Jack, Connelly, & Morris, 2012).

Unlike sequence variations, which are relatively stable across an individual's lifetime, there is emerging evidence that epigenetic modifications may occur dynamically in response to situational conditions. Immediately following a stressful experimental task, for instance, the methylation status of the stress-associated gene *OXTR* first increases, and then once the stressor ends, methylation status decreases below baseline (Unternaehrer et al., 2012). Epigenetic mechanisms may play an important role not only for long-term influences of environmental conditions on gene expression but also for short-term, rapid changes in gene expression in response to situational social stressors. Basic molecular mechanisms that underlie gene expression thus provide a biological pathway for environmental influences to penetrate deeply, altering patterns of gene regulation and expression.

Advances in molecular biology have greatly increased scientific understandings of the mechanisms through which different social environments lead to changes in gene expression and thus behavior. In addition to investigating potential mechanisms more on the genetic side of the G × E equation, our perspective is that incorporating a cultural approach in the G × E framework adds the richness of cultural content to the environment side of the equation and may ultimately elucidate some of the psychological processes underlying G × E effects.

## Gene–Culture Interaction Framework

Building on the gene–environment framework, the gene–culture interaction (G × C) approach provides one possible way of reconceptualizing the environment to include the cultural context (Kim, Sherman, Sasaki, et al., 2010; Kim, Sherman, Taylor, et al., 2010; Kim et al., 2011). The "environment" in the G × E framework is a broad concept that can include anything from resource availability and weather variability to social environments in the family and the local society. Types of social environments can then be meaningfully partitioned into the *personal environment*, or individual variation in experiences and events such as stress in the home setting (e.g., Taylor et al., 2006), and the *cultural environment*, or beliefs, values, practices, and products that constitute a shared system of meaning, such as the Western emphasis on independence and personal choice (e.g., Markus & Kitayama, 1991). Although there are many ways to potentially parse the environmental component of G × E, we argue that focusing on the cultural part of the environment, as in the gene–culture interaction framework, is particularly important both theoretically and practically.

Although no one definition of culture is uniformly agreed upon, there are key components that many scientists are likely to endorse. Most would agree that culture is nonbiological—that is, nongenetic. Via evolutionary processes, social organisms may be biologically prepared with the capacity to develop culture (Tooby & Cosmides, 1992), and genes and culture may interact (Dressler, Balieiro, Ribeiro, & Dos Santos, 2009; Kim, Sherman, Sasaki, et al., 2010; Kim, Sherman, Taylor, et al., 2010; Kim et al., 2011; Kitayama et al., 2014; Sasaki, Kim, & Xu, 2011) and mutually influence each other in processes of gene–culture coevolution (Chiao & Blizinsky, 2010; Feldman & Laland, 1996; or dual inheritance: Boyd & Richerson, 1985; see also Cavalli-Sforza & Feldman, 1981; Durham, 1990, 1991; Fincher, Thornhill, Murray, & Schaller, 2008; Lumsden & Wilson, 1981) to ultimately shape the neural processes underlying thought and behavior (see Chiao & Immordino-Yang, 2013). At the same time, however, culture can be separated from genes. Although culture influences and is influenced by biological processes, culture itself can be understood as beliefs, values, practices, and products that are socially created rather than genetically inherited by living beings (de Waal, 2001). Once socially created, these environmental features must then be socially transmitted to others and passed down over multiple generations such that they are maintained well beyond the lives of their original creators (Berger & Luckman, 1966). These characteristics, some have argued, are among the hallmarks of culture (de Waal, 2001; Geertz, 1973; Herskovits, 1948; Triandis, 2007).

Culture exists not only outside the self in the form of cultural products, or tangible, public representations such as art and media, but also inside the mind (Cohen, 2009; Kim & Markus, 1999; Shweder, 1995). In our approach, the G × C interaction framework incorporates both aspects of the cultural environment. Thus, consideration of culture as a form of environment provides an understanding of how an individual's own beliefs and values are shared with others and how these mutually shared meanings allow people to interpret events and understand their experiences. Shared meaning constitutes an important part of culture that is unique from other forms of environment and is one of the main strengths of considering cultural and psychological factors in G × E research.

## Mechanisms of the Gene–Culture Interaction Framework

Although the biological mechanisms of G × C interactions have yet to be clearly elucidated, some of the known biological mechanisms of G × E interactions may suggest possible mechanisms linking the cultural environment to genes. One way of conceptualizing culture is as socially shared patterns of mental processes and psychological responses, which can be applied to the process of social signal transduction. Just as the subjective perception of social conditions can affect patterns of gene expression (Slavich & Cole, 2013), differences in cultural expectations and norms could potentially affect perceptions of social situations and thus the way genes are expressed. For example, in the case of seeking social support, European Americans are more likely to confide in close others in distressing situations and directly ask for help compared to Asian Americans, who may be relatively more concerned about burdening their social networks (Kim, Sherman, & Taylor, 2008; Taylor et al., 2004). Thus, the same social situation—seeking social support—could be perceived as more or less threatening depending on the cultural context (Taylor, Welch, Kim, & Sherman, 2007). One possibility is that such cultural variation in subjective experience could manifest in cultural differences in the activity of gene expression.

Cultural meanings, practices, and patterns of interactions could also have implications for epigenetic processes. Epigenetic differences in the genomes of monozygotic twins, for instance, can occur as a function of accumulated exposure to divergent life experiences (Fraga et al., 2005). Such epigenetic modifications result in different behavioral and health outcomes—in this case, differences between twins in disease onset. Similarly, individuals engaged in different cultural contexts may be systematically exposed to varying experiences that contribute to epigenetic change. For instance, a study comparing

Asia and North America found that the cultural environment of the United States offered more frequent and potent opportunities to exert influence on one's surroundings compared to Japanese cultural environments, which provided more opportunities for adjusting to the situation (Morling, Kitayama, & Miyamoto, 2002). A lifetime of exposure to varying experiences could potentially result in culturally differing patterns of methylation, epigenetic modifications that in some cases may be transmitted across generations, providing an inheritance mechanism for the impact of environmental factors (see Franklin & Mansuy, 2010).

From the perspective of differential susceptibility, individuals may exhibit differences in their genetic predisposition to methylation and thus be more or less sensitive to environmental influences (e.g., Huang, Perry, & Laux, 1999). In a study of adults with traumatic experiences, increased methylation leading to decreased gene expression was found to moderate the association between serotonin transporter gene polymorphisms and depressive symptoms (van IJzendoorn, Caspers, Bakermans-Kranenburg, Beach, & Phillbert, 2010). The short variant of the *5-HTTLPR* gene predicted more feelings of unresolved loss but only when methylation levels were low. Thus, epigenetic processes, such as methylation, may operate at the interface of environmental exposure and psychological outcomes.

## Evidence for Gene–Culture Interactions

Evidence for G × C interactions relevant to health outcomes derives from studies investigating a variety of genes and psychological processes. Building on the idea of environmental susceptibility, G × C interaction research focuses on genes that have been implicated in environmental sensitivity and predicts that particular genetic variations will alter an individual's susceptibility to environmental influence. In a study of the interaction between variants of the 2A serotonin receptor (5-HT2A) and depressive symptoms, the perception of one's family as a prototypically "good family" in Brazil negatively correlated with depressive symptoms (Dressler et al., 2009). The effect was enhanced for those individuals carrying the AA variant of 5-HT2A compared to individuals with AG or GG variants. Another study, which investigated G × C interactive effects on psychological well-being, found that religiosity was associated with greater well-being for those genetically predisposed to be environmentally sensitive (i.e., those carrying the GG variant of a particular oxytocin receptor gene polymorphism), but only for those from a cultural context in which religion tended to provide more frequent opportunities for affiliation (Sasaki et al., 2011).

Gene–culture interactions have also been shown for health-relevant behaviors, such as emotion regulation. Kim and colleagues (2011) compared emotion regulation approaches between the United States, where expressivity is more highly valued, and Korea, where suppression is valued more. Koreans with the environmentally sensitive variant (GG genotype) of the oxytocin receptor gene (*OXTR*) reported using more emotion suppression than those with the AA genotype, whereas European Americans showed the opposite pattern. Overall, it seems that through engagement in different cultural systems, individuals genetically predisposed to environmental sensitivity are the ones to most strongly adopt the particular psychological and behavioral patterns supported by a culture for certain psychological phenomena (Kim & Sasaki, 2012, 2014). Likewise, when comparing across multiple cultures, the most culturally divergent patterns of behavior relevant to a gene of interest appear to emerge among people with environmentally sensitive predispositions.

## Bridging Gene × Culture with Gene–Culture Coevolution

Although the gene–culture interaction and gene–culture coevolution perspectives both investigate the relationship between biological and cultural variation, they address different aspects of this relationship, and there are some interesting points that arise from comparing these perspectives. Gene–culture coevolution theory (also known as dual inheritance theory) provides an explanation for the macro-level interactions between culture and genes by applying a Darwinian selection framework to culture. The theory proposes that similar to genetic variants, features of a culture could increase individual fitness and be transmitted through social learning in a system of inheritance not unlike genetic inheritance (Boyd & Richerson, 1985; Chiao & Blizinsky, 2010; Feldman & Laland, 1996). Thus, cultural features, which serve as adaptations to local environments and conditions, could evolve much like genes evolve. Such cultural evolution may have been particularly important in the history of human evolution because cultural practices could have allowed for adaption to environments at a pace much faster than allowed by genetic evolution alone.

According to gene–culture coevolution, cultural systems contribute to creating environmental pressures under which genetic evolution occurs. One classic example is the coevolution of dairy farming practices and the lactase gene. The ability to digest milk proteins usually disappears after childhood. However, there is an association between a history of dairy farming and the frequency of genetic variants related to lactose tolerance in a population (Beja-Pereira et al., 2003; Myles et al., 2005), suggesting that the development of cultural practices supporting dairy farming and milk consumption contributed to evolutionary selection favoring alleles for adult lactose tolerance. Another example derives from research investigating the association between individualism–collectivism tendencies and the serotonin transporter gene polymorphism *5-HTTLPR* (Chiao & Blizinsky, 2010; for gene–culture coevolution evidence of cultural tightness vs. looseness and *5-HTTLPR* as explained by historical ecological threat, see Mrazek, Chiao, Blizinsky, Lun, & Gelfand, 2015). Previous studies have demonstrated that regions with historically greater pathogen prevalence tend to be more collectivistic (Fincher et al., 2008). Chiao and Blizinsky (2010) report that the cultural value of collectivism, which enhances social connectedness, is associated with a higher frequency of the s allele of *5-HTTLPR*, which has been linked to anxiety and mood disorders in certain populations. The development of collectivistic practices may have evolved to reduce exposure to environmental pathogens and thus may have also strengthened selection pressures for the s allele of *5-HTTLPR* if it buffers susceptible populations against genetic predispositions for affective disorders (see also Way & Lieberman, 2010).

The theory of gene–culture coevolution is complementary with the gene–culture interaction framework in that the two approaches operate at different levels of analysis. Gene–culture coevolution focuses on the macro-level evolutionary processes shaping cultural norms and genetic variants. In contrast, the gene–culture interaction framework addresses how culture and genetics interact to influence behavioral and psychological outcomes at the individual level. Through gene–culture coevolution processes, a particular adaptive cultural value may become common within a population, creating selective pressures for a particular genetic variant. However, genetic variation will still exist in the population. The gene–environment interaction framework explains how individuals within the same cultural context might think and behave differently depending on their genetic predispositions. For example, there may be a region-level correlation between the prevalence of the s allele of *5-HTTLPR* and collectivistic values (Chiao & Blizinsky, 2010), whereas at the individual level, s allele carriers versus l allele carriers may be influenced by cultural norms differently, as predicted within the gene–culture interaction framework.

Research on gene–culture interactions is new, yet the perspective holds great promise for illuminating the processes underlying genetic and environmental influences on behavior. Investigations in molecular biology may inform understandings of underlying biological mechanisms, whereas cultural research may contribute to predictions about underlying psychological mechanisms. By bringing these two perspectives together, gene × culture research may offer a more complete picture of the process through which cultural information, both inside and outside the head, can interact with genetic information to lead to different outcomes.

## Theoretical Issues and Questions Raised by Gene × Culture Research

As an emerging area of research, gene–culture interactions raise a number of important issues with theoretical relevance. First, there are some general patterns of results from gene × culture research that may have implications for cultural psychology. Second, research on genes and culture raises interesting questions about genetic frequencies in different populations. Especially for addressing issues related to health, the combination of both genetic and cultural considerations holds great potential. Yet at the same time, the gene × culture framework represents a departure from more classic cultural perspectives in some ways and raises important questions to be addressed.

### *Implications for Cultural Psychology*

Gene–culture interactions offer a way of understanding not only how genetic predispositions may manifest themselves differently depending on the cultural context but also how cultural factors may influence people differently according to individual differences at the level of genes. This framework captures how the content of culture can inform research in the realm of biology and behavioral genetics. However, that is not to say that the influence of culture is unvaried. Genes may constrain the effects of culture by providing people with a range of possible traits or behaviors, and the environment, including culture, can then select from that range of possibilities to lead to a particular outcome.

Gene × culture findings have shown that some well-known cultural effects seem to occur more for people with certain genetic predispositions than others. Cultural differences in emotional support seeking (Kim, Sherman, Sasaki, et al., 2010) and emotion regulation (Kim et al., 2011), for instance, emerge among people with GG and AG genotypes of *OXTR* but not AA genotypes. In addition, previously found cultural differences in locus of attention (Choi, Koo, & Choi, 2007; Masuda & Nisbett, 2001) appeared only for GG and CG genotypes of *5-HTR1A* and not for CC genotypes (Kim, Sherman, Taylor, et al., 2010). This general pattern of results may have implications for cultural psychology more broadly because it is possible that many previously discovered cultural differences are stronger for those with certain genetic predispositions than others. Although it is probably not the case that a single gene leads people to be more or less culturally normative across all traits and behaviors, one possibility given our G × C findings and other G × E research is that sets of genes (e.g., oxytocin-related genes) may be related to culturally normative responses for specific outcomes (e.g., socioemotional sensitivity). This means that cultural differences on these outcomes may be more pronounced for people with certain genetic predispositions than others, but across outcomes, there should be no relationship between cultural normativity in general and any one set of genes, consistent with insights on why cultural differences are not always reducible to individual differences (Na et al., 2010).

### *Covariation of Cultural and Genetic Differences*

One intriguing question derives from observations combining cultural differences in psychological and behavioral tendencies with differences found in the distribution of specific genotypes across ethnic groups, such as people of East Asian versus European ancestry. Interestingly, many of the genes that have been commonly studied in psychology, such as *5-HTTLPR, OXTR*, and *DRD4*, have drastically different genotype distributions across ethnic groups. Sometimes these divergent genotype frequency distributions correlate with documented differences in cultural norms (Chiao & Blizinsky, 2010; Mrazek et al., 2015). However, when one considers the general set of psychological tendencies associated with any given polymorphism, the way in which genotype distributions within a cultural group align with their documented psychological tendencies varies considerably.

For instance, compared to groups with European ancestry, East Asian samples tend to have a much higher frequency of the *5-HTTLPR* polymorphism s allele, which is associated with stress reactivity (e.g., Caspi et al., 2003). East Asians are also known to be more avoidance oriented than North Americans with European cultural backgrounds (Heine et al., 2001; Lee, Aaker, & Gardner, 2000). Thus, the fact that the environmental susceptibility genotype of *5-HTTLPR* is more common among people from East Asian cultures, which emphasize interpersonal influence (Morling, Kitayama, & Miyamoto, 2003) and the value of group harmony (Kim & Markus, 1999), seems to make sense intuitively.

At the same time, the G allele of *OXTR* rs53576 polymorphism is far more common among European Americans than among East Asians (e.g., Kim, Sherman, Taylor, et al., 2010; Kim et al., 2011). Given the association of the *OXTR* G allele with social bonding and affiliation (e.g., Bakermans-Kranenburg & van IJzendoorn, 2008; Rodrigues, Saslow, Garcia, John, & Keltner, 2009; but see Bakermans-Kranenburg & van IJzendoorn, 2014), as well as with greater environment susceptibility (Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2007), it may seem counterintuitive to find a higher frequency of G alleles among European Americans, who are from cultural contexts that tend to emphasize independence and individualism, than among East Asians, who are from cultural contexts in which interdependence and collectivism are fostered.

To further complicate the matter, different variants of *DRD4* polymorphism (i.e., 2-repeat and 7-repeat alleles) in different ethnic groups are associated with similar functional and psychological characteristics (Reist et al., 2007; Wang et al., 2004), but the frequencies of these respective environment susceptibility genotypes are roughly compatible between European Americans and Asians (e.g., Kitayama et al., 2014; Sasaki et al., 2013).

Genetic profiles of different ethnic groups are no doubt the result of natural selection processes and specific challenges posed by the regional environment, but it is beyond the scope of this chapter to address how particular genes come to be more frequent in one ethnic group than another. In this chapter, we focus on what we can learn from the observation of diversity in genetic distributions among different ethnic groups and future research questions that may be inspired by these observations.

Given that the frequencies of genotypes for these susceptibility genes differ greatly, and sometimes against what seems to be the intuitive association with cultural tendencies, one can reasonably infer that cultural tendencies cannot be simply explained as averages of phenotypic tendencies of populations. That is, the frequency distribution of *OXTR* genotypes (Kim, Sherman, Sasaki, et al., 2010; Kim et al., 2011) probably does not explain why East Asians are more interdependent than European Americans. To the extent that there is any relationship between genotypic distributions and cultural tendencies, the relationships will be considerably more complicated, as proposed by other theoretical models such as gene–culture coevolution and gene–culture interaction. For example, there is evidence that the *DRD4* variant may moderate the cultural difference in independent versus interdependent social orientations such that 2- or 7-repeat allele carriers tend to have greater independence for European Americans but greater interdependence for East Asians (Kitayama et al., 2014).

An additional point is that it is not always clear how specific the associations are between a gene and its psychological correlate. For example, stress reactivity is often discussed in relation to *5-HTTLPR*, although it is by no means the only gene that is associated with stress reactivity. There are other genes, such as *OXTR* (Rodrigues et al., 2009) and *MAOA* (Caspi et al., 2002), that influence one's sensitivity to environmental distress. Thus, although there seems to be some genetic specificity in the associations with different social behaviors, strongly inferring conceptually distinct and exclusive psychological outcomes from specific genes should be done with caution. Rather, there may be sets of genes with distinguishable but overlapping functions that predispose individuals to certain domains of sociocultural influence. It will be useful to adopt more reliable ways of investigating genetic influence, such as a polygenic approach examining the link between a trait and multiple genes and a pleiotropic approach examining how a single gene may be linked to multiple traits.

Moreover, considering gene–culture interactions in the context of genotypic distribution differences in ethnic groups raises the question of why sometimes only a small genetic minority in a cultural group seems to embody culturally normative tendencies. For example, the s allele of *5-HTTLPR* is relatively rare among European Americans, and the G allele of *OXTR* rs53576 is relatively rare among East Asians, yet both the *5-HTTLPR* s allele and the *OXTR* G allele seem to predispose people to be more susceptible to cultural influences. For this question, we propose that there are at least two possible answers.

One possibility is that the maintenance of culturally normative tendencies may be shaped by multiple genes in conjunction with each other. Examination of multiple polymorphisms in combination, including genes that are more or less common in a given population (e.g., G allele of *OXTR* or s allele of *5-HTTLPR* among East Asians), is likely to yield a more normally distributed genetic profile at the cultural group level (cf. Belsky et al., 2013), evening out skewed distributions of each polymorphism. In other words, the genetic basis of cultural susceptibility itself is probably similarly and normally distributed among many cultural groups. Given that, it would be unwise to infer that any single gene is responsible for a broad range of cultural differences or that a gene or even a group of genes are responsible for a broad category of social behaviors, such a cultural conformity, without further specifying the exact processes. It is more likely that a particular gene or set of genes predispose each individual to be sensitive to a small aspect of cultural environment, and only as a whole, we may be able to see cultural patterns.

This issue of single gene research is not limited to research in cultural genetics. The single gene approach has been fruitful in leading the initial examination of the excruciatingly complex process of genetic influence, allowing investigators to formulate theory-driven predictions in a relatively parsimonious manner. However, the field is moving toward examining how multiple genes together influence psychological and behavioral tendencies. Yet, there is currently no clear model to examine multiple genes in conjunction with each other. It is unclear if the genes function in additive, interactive, or compensatory ways, although there are some notable efforts to deal with this issue. For example, Belsky and colleagues (2013) selected multiple genes based on results of genome-wide association studies (GWAS) and examined how they predict particular health-related behaviors, such as smoking and obesity, using an additive model. Also, genome-wide complex trait analysis (Yang, Lee, Goddard, & Visscher, 2011) was developed to address the "missing heritability" problem as a way to utilize GWAS data for estimating and partitioning complex trait variation. Although these models offer promise, to date there has not been a compelling study using multiple genes along with environmental input to predict social behaviors.

As the field moves forward, there will no doubt be empirically and biologically informed ways to examine multiple genes to further uncover the role of genes and environment in shaping social and cultural behaviors, and researchers will then be able to answer questions with greater certainty.

An additional possibility is that much of the culture-specific norms have not been stable for long enough to be reflected directly by a set of genes. The time frame for genetic divergence among ethnic groups is more than 40,000 years (Bowcock et al., 1991). Thus, much of the genetic composition of each ethnic group seems to predate certain components of the established culture, at least in terms of cultural values, institutions, and assumptions based on specific historical antecedents. Of course, as research on gene–culture coevolution shows, cultural practices may have a detectable influence on genetic distribution in specific cases (e.g., Beja-Pereira et al., 2003) within a relatively brief evolutionary time frame. Nevertheless, it is likely that changes in thoughts and behaviors at the individual level, and even cultural practices and norms at the group level, are much more malleable and quick-paced than changes in genetic characteristics of populations. Given that, the link between genetic profiles of a particular ethnic group and their cultural characteristics may be fairly unstable, and this is an important possibility to keep in mind.

The ways in which genes and culture are related with each other are numerous, as shown in this very brief review. Currently, much remains unknown in terms of how genes work to eventually lead to traits, and there are a number of caveats to consider in formulating new theories. The field will benefit in the future from combining multiple perspectives, including psychology, behavioral genetics, population genetics, and anthropology, to address questions about the mind and behavior.

## How Can the Gene × Culture Framework Be Applied to Health Research?

Due to the growth of cultural psychology, there is now a relatively large body of research to draw upon for investigations of health using a gene–culture interaction perspective. In this final section, we discuss cultural research relevant to health, promising avenues of future research, and implications for public health policy.

### *Culture and Health*

Cultural differences exist even in basic psychological phenomena, many of which have important implications for understanding what people consider healthful and how they ultimately achieve positive health outcomes. For instance, it is well-known that social relationships have strong implications for health (Cohen, 2004), and this general link may be true in every culture. The meanings embedded in relationship contexts, however, may vary across cultures and thus have relevance for understanding a range of health-related issues, from the way people draw on their social networks to cope with difficulties (Kim et al., 2008) to the extent to which one's well-being is contingent on others (Plaut et al., 2012). In addition, given that certain genes or sets of genes may be linked to social sensitivity in particular contexts (e.g., Bartz, Zaki, Bolger, & Ochsner, 2011), it may be especially useful for gene–health research to consider the cultural contexts that shape norms and expectations in social relationships.

Research from a cultural perspective has also shown more directly that there are cultural differences in health outcomes, the willingness to seek different kinds of treatment, and the effectiveness of different treatments. Given that perceived discrimination contributes to health disparities (Major, Mendes, & Dovidio, 2013; Pascoe & Smart Richman, 2009; Williams & Mohammed, 2009), it is important to consider intergroup dynamics for investigations on culture and health. For instance, it is well documented that people from lower social class contexts tend to fare worse than those from a higher social class on certain health outcomes, in part due to greater exposure to stress and other health-debilitating risks (Williams & Collins, 1995; for review, see Matthews & Gallo, 2011). In addition, minorities may seek mental health treatment less often compared to majority group members, even after acculturating to a new culture (B. Kim, 2007; Mills, 2012), and for those who do seek medical care, there is evidence that ethnic minorities tend to receive lower-quality treatment on average (Williams & Sternthal, 2010). Some minority groups, such as Black Americans, continue to face lower average life expectancies compared to White Americans, even after taking social class into account (Williams & Sternthal, 2010), raising the possibility that minorities may face greater health risks due to perceived discrimination. However, some immigrant groups, such as those with Mexican backgrounds, tend to have equivalent or better health outcomes than the mainstream White population, despite the fact that they face greater risk of poverty and low-quality health care (a phenomenon termed the "Hispanic paradox"; Markides & Eschbach, 2005).

People from different cultures may also show different symptomatology for mental health problems and have different beliefs about treatment (Ryder, Ban, & Chentsova-Dutton, 2011). Studies of people with depression across cultures have found that the Chinese tend to somaticize depression symptoms more than do Westerners (Chang, 1985; Tsai, Simeonova, & Watanabe, 2004). Also, European Americans who are depressed tend to show decreased emotional reactivity, whereas East Asians who are depressed show heightened emotional reactivity (Chentsova-Dutton et al., 2007). With regard to support seeking, people from Japan tend to be less likely to seek support from close relationships and from professional services compared to Americans, and this difference may be explained by cultural differences in willingness to disclose problems (Mojaverian, Hashimoto, & Kim, 2013) and relationship concerns, such as disrupting harmony or saving face (Taylor et al., 2004). In addition, a longitudinal study of pregnant women found that the Japanese, compared to Americans, are more likely to experience certain positive pregnancy outcomes when they believe that close others have control over decisions surrounding their pregnancy (Morling et al., 2003). These findings emphasize the importance of understanding how culture may shape the expression or presentation of certain health conditions, as well as how beliefs about appropriate treatment may have consequence for health outcomes.

From the perspective of cultural neuroscience, a more complete picture of how people conceptualize health, make decisions regarding their health, and ultimately achieve positive health outcomes may come from examining the interaction of cultural and biological factors (e.g., Chiao, Cheon, Pornpattananangkul, Mrazek, & Blizinsky, 2013). Gene–culture interactions may be a particularly promising area of research within cultural neuroscience that explains diverse psychological responses (Sasaki, 2013). For example, research suggests that situating the individual within an intergroup context may potentially have implications for health and that people with certain genotypes may be more sensitive to stressful features of this context than others. Specifically, research by Cheon and colleagues (2014) found that people who had prior negative contact with out-groups and perceived that the social world is dangerous were more likely to report intergroup biases, but this relationship was stronger for carriers of the more stress- or threat-sensitive s allele of *5-HTTLPR* compared to those homozygous for the l allele. This research highlights the importance of considering how an individual perceives the self in relation to other groups in an intergroup context, as well as one's genetic predispositions to be sensitive to stress in this context.

Genes represent one component of biology but are certainly not the only important factor to consider for questions surrounding health. As a field, cultural neuroscience examines the complex ways in which culture and biology interact (Chiao & Ambady, 2007), and it is crucial to consider specific findings of gene–culture interactions within the context of cultural neuroscientific frameworks more broadly in order to understand health disparities (Cheon, Mrazek, Pornpattananangkul, Blizinsky, & Chiao, 2013; Chiao et al., 2013). A recent review of cultural neuroscience (Kim & Sasaki, 2014) proposes a framework for understanding how genetic and environmental inputs affect psychology via neural processes and how culture shapes these processes at multiple levels and is constrained by the processes of evolution. Because it is clear that culture plays a role in health outcomes in multiple ways, the next challenge for future research is to incorporate a cultural approach while anchoring findings within a broader theoretical framework.

### *Future Research on Gene–Culture Interactions*

There are many ways to conceptualize culture (Cohen, 2009), and future research on gene–culture interactions should thus explore other methods of examining culture in addition to using cultural group comparisons. For instance, measures of subjective experience may be one way to consider culture in investigations. As previously described, a G × C study of cultural consonance, or the degree of match between one's own life and the broader shared culture, found that lower cultural consonance was associated with greater depressive symptoms, and this was especially the case for people with a potential genetic link to depression-related conditions (Dressler et al., 2009). This study raised the important point that disparities between subjective experiences and the norms prescribed by the broader culture can have implications for health outcomes.

Other cultural psychological approaches include cultural task analysis to test implicit indicators of cultural differences (Kitayama, Park, Sevincer, Karasawa, & Uskul, 2009), continuous measures of educational attainment to measure social class as culture (Grossmann & Varnum, 2011), and cultural priming to test causal effects of cultural information on psychological outcomes (Hong, Morris, Chiu, & Benet-Martínez, 2000; Oyserman & Lee, 2008). Cultural priming may present an especially promising future direction for gene–culture interaction research because it allows for causal inferences about the relationship between cultural information and an outcome for people with different genetic predispositions (for a G × E example of environmental priming in a laboratory setting, see Sasaki et al., 2013). All these examples of cultural approaches could potentially be used in conjunction with the G × C framework.

Future research should also examine the mechanisms through which gene–culture interactions occur, and the G × C framework may provide good opportunities to address this issue. The framework of G × C, like that of G × E, makes predictions about moderation by formalizing how the same genetic predisposition can be linked to different outcomes depending on one's culture and also how the same cultural background may predict different outcomes depending on one's genetic predisposition. As Baron and Kenny (1986) explained, the best moderators are those that suggest possible mediators, revealing something about the underlying mechanisms involved in a psychological phenomenon. Culture is a moderator with such potential because numerous cultural psychological studies have revealed mediating processes. In research on culture and motivation, for instance, Heine and colleagues (2001) initially established an interaction between a situation (receiving success vs. failure feedback) and culture (Japan vs. North America) on task persistence and additionally showed that the interaction seemed to suggest motivation as a potential mediator. Specifically, they showed that North Americans seemed to experience greater motivation following success (vs. failure) feedback, allowing them to persist more on a task compared with Japanese participants. On the other hand, Japanese participants seemed to be more motivated by failure than success compared with North Americans. Furthermore, cultural differences in motivation were explained by between-group differences in lay theories about the utility of effort. Because cultural differences in a given outcome (e.g., task persistence) pointed to differences in an underlying process (e.g., motivation) and revealed potential explanations for cultural differences (e.g., lay theories), this example illustrates how a cultural approach can be useful for elucidating basic psychological processes.

A similar approach can be used in the context of health for G × C research. For example, one of our previous G × C studies described previously found that culture moderates the link between *OXTR* and emotional seeking among those who experience greater distress (Kim, Sherman, Sasaki, et al., 2010). This finding of cultural moderation could potentially illuminate social processes in relation to oxytocin more broadly because it suggests that people who may be predisposed to be more socially sensitive only directly seek more emotional social support in cultural environments that endorse this behavior as appropriate. Although initial oxytocin findings seemed to suggest that higher levels of oxytocin generally encourage people to socially connect with others in positive ways (Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005), later research has demonstrated that oxytocin can also have negative effects, particularly in the context of in-group–out-group competition (De Dreu, Greer, Van Kleef, Shalvi, & Handgraaf, 2010; Declerck, Boone, & Kiyonari, 2010) or for individuals lacking optimal resources to deal with social stressors (Bartz, Zaki, Bolger, et al., 2010; Bartz, Zaki, Ochsner, et al., 2010; Bartz, Simeon, et al., 2011). In reality, the influence of oxytocin is complicated and should therefore be applied with caution (Miller, 2013). The social effects of oxytocin appear to be highly dependent on aspects of the context and the individual (for review, see Bartz, Zaki, et al, 2011); in addition, our research suggests that oxytocin may lead people to interact with others in ways that are sanctioned by the sociocultural context (Kim, Sherman, Sasaki, et al., 2010; Kim et al., 2011; Sasaki et al., 2011).

These G × C findings further support theories about how social support processes may not function in the same way across cultures, and more broadly, they demonstrate that genetic predispositions may manifest themselves in different ways according to what is normative in the cultural context. As in the case of the culture, *OXTR*, and emotional support-seeking study described previously (Kim, Sherman, Sasaki, et al., 2010), the act of seeking emotional social support can have different meanings depending on the cultural context (for review of culture and social support processes, see Kim et al., 2008). G × C research demonstrates that the relationship between genetic predispositions and behaviors may depend on the cultural meanings of behaviors rather than on actual behaviors per se.

## *Implications of Gene × Culture Research for Public Health Policy*

The utility of G × C research goes beyond the advancement of theory and development of new methodology; it also has practical applicability to health issues, particularly in its ability to inform public health policy. Here, we explore how G × C research can be applied to the policy areas of defining health and developing goals for public health policy and providing effective care in a targeted, cost-efficient manner. In so doing, we also discuss implications and potential recommendations based on past studies and identify questions for future research to address.

### DEFINING AND DELIVERING HEALTH

Before developing policy, public health policymakers throughout the world should address the following questions: What constitutes optimal health? How is it best fostered in a given population? Answering these questions is far from straightforward, and much research on cultural differences strongly suggests that peoples' responses to these questions can vary in important ways. The World Health Organization's (WHO) recent emphasis on addressing "social determinants of health," or social factors that contribute to health inequities throughout the world (Commission on Social Determinants of Health, 2008), is consistent with this idea that effective public health policy must take the sociocultural context into account. WHO also defines health as "a state of complete physical, mental, and social well-being and not merely the absence of disease or infirmity" (World Health Organization, 2003), bug across cultures, the meaning of well-being might vary greatly. For example, a study of conceptions of health in New Mexico and Colorado found that Hispanic villagers highly emphasized fulfilling role obligations according to one's age and sex, and the primary repercussion of illness was that it interfered with the ability to fulfill one's obligations, not that it affected the sick individual (Schulman & Smith, 1963). When addressing the concept of health among First Nations or Aboriginal North Americans, a common model is the medicine wheel, which depicts health as a holistic balance among social, mental, physical, and spiritual elements—the latter being a factor that does not commonly appear in Western concepts of health (Roberts, Harper, Tuttle-Eagle Bull, & Heideman-Provost, 1998; Waldram, 2006). Furthermore, cultural variation also exists in the conception of a specific component of health—that is, mental or subjective well-being (Fulmer et al., 2010; Oishi & Diener, 2003; Uchida & Kitayama, 2009). Lay concepts of subjective well-being in Western cultures often tend to center on the "pursuit of happiness" and avoidance of unhappiness for oneself (Diener & Diener, 1995; Suh, Diener, Oishi, & Triandis, 1998). In some Eastern cultures, however, subjective well-being is achieved through fulfilling role obligations and finding a balance between happiness and unhappiness (Lu, 2005; Suh et al., 1998; Uchida & Kitayama, 2009). These findings suggest that public health policy aimed at highly maximizing the population's happiness may increase the psychological well-being of a Western population, but it may not have the same effects in an Eastern population, where such policy may be less appropriate.

Beyond considerations of the definitional components of health, cultural psychological research also sheds light on differences in the ways to achieve optimal health. For example, Eastern cultures' emphasis on balance and dialecticism might apply to attitudes toward health and the desired goals of public health. In research on topics such as emotional experience (Uchida & Kitayama, 2009), reasoning and logic (Ji, Nisbett, & Su, 2001; Peng & Nisbett, 1999), and self-concept (Heine & Lehman, 1997; Spencer-Rodgers, Williams, & Peng, 2010), it has been shown that Asians tend to be more tolerant of contradiction, think of events in terms of cycles rather than linearly, and place importance on the balance of opposing forces that are viewed as mutually dependent. It is possible, then, that learning to accept illness and disability when they occur is an important part of achieving health in some Asian populations. The issue of achieving optimal health is further complicated by the possibility that cultural differences in certain phenomena may be moderated by genetic predispositions (Kim & Sasaki, 2014). Thus, policy aimed solely at eradicating illness and disability may be incomplete, missing important differences in cultural attitudes and beliefs and the possibility that these cultural differences could potentially vary by genes.

However, it is also important to consider the individual differences that exist between people within a culture. People may have certain predispositions in terms of their biology, personality, and behavior; thus, it will be important for public policy to allow for flexibility in accommodating within-group variation. For example, individual differences in extraversion versus introversion have been linked to a dopamine receptor gene, *DRD2*, with carriers of the A1 allele being significantly more extraverted than noncarriers (Smillie, Cooper, Proitsi, Powell, & Pickering, 2010). People who vary on levels of extraversion would likely also differ in the types of situations and behaviors that best foster social and mental well-being (Diener, Oishi, & Lucas, 2003; Moscowitz & Coté, 1995). In terms of health policy, what may contribute to optimal health for a more extraverted A1 allele carrier, for instance, may not work as well for someone without this allele. It is a further possibility that genes may express themselves differently depending on a person's cultural environment (e.g., Kim, Sherman, Sasak, et al., 2010); thus, a thorough understanding of how best to promote the health of a population may require policy that takes both individual predispositions and cultural influences into account.

### PROVIDING EFFECTIVE, EFFICIENT CARE

Whether implemented at the local, regional, or national level by governments and institutions, public health policy aims to promote health and prevent disease and illness in a population. Due to the spread of health-related ideas and tools throughout the world, people are sometimes faced with the challenge of adapting policy that has been imported from other populations. However, effective policy involves far more than finding a one-size-fits-all prescription for well-being. Policy must be tailored to fit various types of populations, within which there will be differences in genetic predispositions and cultural backgrounds. Although a highly personalized care system may be ideal for allowing each person in a society to strive for better health in his or her own way, the reality is that public health policy is bound by limited resources and is therefore under pressure to maximize its efficiency. Negotiating a balance between the ideal of effective, personalized care and the limitations surrounding its provision is a difficult challenge for public health policymakers, but helping to do so may be one of the greatest promises of G × C research.

There is much public interest in genetics as a potential tool to identify health risk factors. Although such an approach has much promise, G × C findings caution against the assumption that genetic associations with health outcomes are uniform. The findings of G × C research provide a more nuanced understanding of how multiple factors interact in relation to health outcomes, and this knowledge can be used to create more streamlined policy that delivers effective care while limiting the waste of resources. By its mandate, G × C research investigates micro- and macro-level influences on the individual in order to predict outcomes. However, it goes beyond an additive model of these influences, demonstrating how one level moderates the other and uncovering information about potential mediators. In doing so, this research clarifies when predictions based solely on genes or culture are likely to be qualified due to an existing interaction. In terms of health policy, this means preventing the misappropriation of resources that can occur when genes and culture are considered in isolation. To give a hypothetical example, imagine that Japanese policy based on genetic studies conducted in Germany led to individuals with a particular gene being identified as at-risk and given an intervention, when in actuality, that gene was not a risk factor given the cultural environment in Japan. Another example is a scenario in which certain cultural elements in the United States were found to account for a higher prevalence of a disorder in that country, so an intervention policy aimed at widespread change was enacted, even though only people with certain genetic predispositions would be negatively affected. In both situations, the efficiency and effectiveness of policy are compromised by considering genes and culture separately rather than adopting a G × C perspective. Of course, there will certainly be cases in which a person's genes or culture alone may predict a large portion of the variance in certain health outcomes, but G × C research can help predict when any particular association is qualified due to the interaction of genes and culture.

Utilizing a G × C framework can be effective for addressing health issues related to etiology, course, and outcome in different cultures. Clinical depression has been associated with certain genetic precursors, such as the presence of an s versus an l allele of the *5-HTTLPR* polymorphism, depending on the environment: Having an s allele puts one at higher risk of depression if coupled with environmental risk factors, such as loss, interpersonal conflict, or a stressful childhood environment (Caspi et al., 2003; Taylor et al., 2006). As Maselko (see Chapter 23, this volume) explains, various risk factors in the early environment may biologically calibrate a person in a way that can prove maladaptive and increase risk of neuropsychiatric disorders in later life. However, the prevalence and manifestation of depression and other mental health disorders show considerable variability between nations and between groups within nations, suggesting that cultural factors may also play a role in a person's susceptibility (Chiao & Blizinsky, 2010; Kleinman, 1982; Maselko, Chapter 23, this volume; Tsai & Chentsova-Dutton, 2002; see also Chapter 22, this volume). In fact, as Yang and Benson (Chapter 22, this volume) note, clinical diagnoses based on culture-specific symptoms may be more appropriate for determining the actual prevalence of certain disorders. Yet it is not enough to know about the genetic and cultural influences on depression independently if one hopes to predict its occurrence. As discussed in this chapter, genes and culture sometimes interact and therefore should be considered in concert. This has been shown to be the case in depression, as the presence of the s allele of *5-HTTLPR* is actually associated with lower prevalence of the disorder in more collectivistic cultures, perhaps due to the buffering effect of collectivistic cultural values (Chiao & Blizinsky, 2010). Thus, a thorough understanding of how and when not only genetic and cultural factors but also their interactions predict health outcomes can be instrumental in developing effective, efficient policy.

### *Conclusions on Gene × Culture Research and Public Health Policy*

Genes play an important role in determining health risks and outcomes. As such, in matters of how to protect and promote the health of a population, genetic research provides indispensable recommendations about how to create good policy. However, it is important to realize that public health policy is a part of culture—it is an institutional force that shapes and is shaped by the values, norms, and beliefs of a people. Changes made to public health policy change the cultural context in which a population lives. Given that cultural research investigates how the cultural context affects health, it is clear that cultural research on health may have important recommendations for effective public health policy. However, it is not enough to consider genetic and cultural influences on health in isolation and then utilize the information in an additive manner to create policy. In many cases, it is likely that genes and culture interact with each other to influence a person's health, and only future research will be able to determine when this should be expected. Therefore, the G × C framework promises to provide a richer understanding of health for people across diverse societies.

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CHAPTER

# 20

# Epigenetics and Social Behavior

Jessica J. Connelly *and* James P. Morris

**Abstract**

Every cell within a given organism contains the same DNA blueprint; in the case of humans, this means that the same DNA code can give rise to hundreds of different cell types with very diverse functions. The genome accomplishes this feat by organizing the DNA into domains that are transcriptionally active or inactive given the particular cell type and function. This occurs by modification of the DNA and the proteins bound to it; methylation of cytosine residues, DNA methylation, is one such "epigenetic" modification and is the focus of this chapter. The role of epigenetic influences on cultural diversity is poorly understood. Given the natural links between environment and biological function, epigenetic processes are poised to play a critical role in new approaches to understanding the biological underpinnings of culture.

**Key Words:** epigenetics, culture, social behavior, DNA, genome

## Introduction

Every cell within a given organism contains the same DNA blueprint; in the case of humans, this means that the same DNA code can give rise to hundreds of different cell types with very diverse functions. The genome accomplishes this feat by organizing the DNA into domains that are transcriptionally active or inactive given the particular cell type and function (Jaenisch & Bird, 2003; Jenuwein, 2001). This occurs by modification of the DNA and the proteins bound to it; methylation of cytosine residues, DNA methylation, is one such "epigenetic" modification and is the focus of this chapter.

## DNA Methylation as an Epigenetic Modification

DNA methylation is integral in the establishment and regulation of a variety of biological processes. During development, DNA methylation is necessary for mammalian X chromosome inactivation (Riggs, 1975) and the establishment of genomic imprinting (Kurukuti et al., 2006). At the transcription level, DNA methylation has been classically observed at gene promoter regions, where it typically leads to gene silencing; therefore, DNA methylation is thought to regulate gene expression patterns (Bird, 1986). Furthermore, aberrant methylation has also been linked to multiple disease states, the most prevalent of which is cancer (Robertson, 2005). Taken together, DNA methylation has been implicated as important in the establishment of both cellular identity and cellular memory (Holliday & Pugh, 1975; Razin & Riggs, 1980).

DNA methylation involves the addition of a methyl ($-CH_3$) group to the 5-carbon position of the cytosine pyrimidine ring (Figure 20.1). This occurs through the action of DNA methyltransferase enzymes and a methyl donor (*S*-adenosylmethionine) (Bestor, 2000). This 5-methylcytosine modification has been observed to occur most prevalently in cytosine–guanine dinucleotide pairs (CpG) in mammalian, plant,

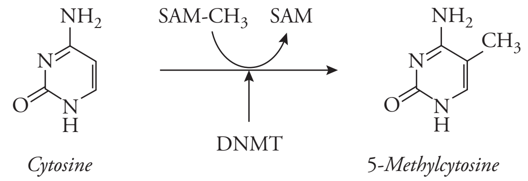

**Figure 20.1** Methylation of a cytosine residue. A methyl group ($CH_3$) is added to the 5 position of cytosine through the action of a DNA methyltransferase enzyme and *S*-adenosylmethionine (SAM).

and several invertebrate genomes (Li & Bird, 2007). In mammals, CpG sites are nonrandomly distributed with high CpG densities clustering at both promoter regions and structural heterochromatin regions, such as telomeres and centromeres (Gardiner-Garden & Frommer, 1987). Globally, however, the mammalian genome is CpG poor, with genomic G–C content estimated at 40% with an observed CpG frequency of 0.8% compared to the expected 4% frequency (Bird, 1986). This decreased frequency has mostly been attributed to the high mutability of 5mC via spontaneous deamination of 5mC to thymidine (Sved & Bird, 1990).

Although highly mutable, CpG methylation is found throughout the genome. Also, although globally the genome is CpG poor, a majority (~60–90%) of the approximately 28 million CpG sites for a given cell type across the nonrepetitive genome are methylated, thus attributing to the assumption that DNA methylation is the default state of the genome (Bird, 1986; Ehrlich et al., 1982; Lister et al., 2009). Certain areas of the genome, however, contain regions of high CpG density. These regions are called "CpG islands" and have been defined by Gardiner-Garden and Frommer (1987) as a greater than 200-base pair region with GC content greater than 50% and CpG ratio greater than 0.6. In the nonrepetitive genome, CpG islands are often found to span promoter regions containing defined transcriptional start sites, and they can also be found in exons, introns, and intergenic regions (Jones, 2012). Interestingly, a majority of the CpG islands that are located at promoter regions adjacent to transcription start sites are nonmethylated in somatic cells (Yoder, Walsh, & Bestor, 1997).

## Tissue-Specific DNA Methylation

Encouraged by genome-wide studies on cellular reprogramming and cancer, a new region of the genome, called CpG island shores, has been annotated. Coined by Dr. Andrew Feinberg and colleagues, CpG island shores are intergenic low CpG dense regions of up to 2000 base pairs that are adjacent to CpG islands and are highly conserved between mouse and human (Irizarry et al., 2009). Demethylation of CpG island shores by chemical or genetic means imports function on these regulatory regions, in that loss of methylation leads to increased gene expression. The methylation level of CpG sites within these regions can be used to distinguish between different cell types, and analyses of different types of cancer show that these same regions alter their origin tissue DNA methylation profile to the profile of other cell types, suggesting the importance of the tissue-specific methylation profile in the maintenance of cell type specificity and the misregulation of this process in cancer.

## Potential Use of DNA Methylation From Peripheral Blood

The focus of this chapter is the use of epigenetic markers to assess endophenotypes of social behavior in humans. The most readily accessible tissue in humans is blood. Although contentious, use of the DNA methylation level from blood has become quite popular in defining phenotypes in social behavior. The controversy is mired in the fact that levels of epigenetic variability in relation to brain phenotype should be measured in the brain because this would be the causal tissue, not the blood. Also, in many cases, there is no relationship between epigenetic variability in the blood and gene expression, which has become an important indicator of the functional significance of epigenetic differences. However, it is important to note that a growing body of literature suggests that there are some epigenetically regulated sites, referred to as metastable epialleles, that are genetically linked or established stochastically early in embryogenesis and persist to a similar degree in all tissues of the body (Finer, Holland, Nanty, & Rakyan, 2011; Harris, Nagy-Szakal, & Kellermayer, 2013; Waterland et al., 2010). It is this type of modification that could be used as a surrogate marker in blood. Human studies comparing DNA methylation levels in the brain and the blood report higher correlation within individuals than between individuals, suggesting that methylation levels from blood may be useful in detecting individual phenotypic variability (Davies et al., 2012; Kaminsky et al., 2011). Other human studies have compared blood and other tissues from the same individual and have identified metastable epi-alleles (Kaminsky et al., 2011). There is a growing body of research in human social behavior that suggests the utility of the measurement of DNA methylation from blood in relation to social phenotype. The use of these measurements, their interpretation, and their usefulness in defining variable human phenotypes are discussed next.

## DNA Methylation and Individual Variability

### *Defining Individual Variation*

Humans are a diploid organism—that is, every cell contains two copies of each chromosome and, therefore, two copies of each gene; each gene copy is called an allele, and each allele can be methylated. In a single cell, the level of methylation at a single CpG site can be 100% (both alleles methylated), 50% (one allele methylated), or 0% (neither allele methylated), as shown in Figure 20.2A. When we examine methylation in a tissue, which is made up of many cells (and often many cell types), we generate an overall percentage methylation for that tissue that is a reflection of the combined methylation level across all of these cells (Figure 20.2B). For example, if an individual is 50% methylated in a given tissue, this could reflect the following possible single cell-level methylation status: (1) All of the cells assayed are methylated at one allele; (2) half of the cells are methylated at both alleles and the other half of the cells are not methylated at either allele; or (3) one-fourth of the cells are methylated on both alleles, one half of the cells are methylated on one allele, and the last fourth of the cells are not methylated at all. In reality, the same CpG site when assayed in the same tissue in many individuals can vary from 0% to 100%. An example of this is shown in Figure 20.3. DNA methylation levels at two CpG sites in the *OXTR* gene were measured in DNA derived from peripheral blood mononuclear cells taken from 576 individuals. Each dot on the graph represents a single person's methylation level at that site. These data clearly indicate that methylation level is variable in the general population at these sites and that the level of methylation differs at these two sites even though they are only 10 base pairs apart. However, the level of methylation between these two sites within individuals is highly correlated (Spearman's rho = 0.64, $n = 576$, $p < .0001$). Individual epigenetic variability has been reported (Fraser, Lam, Neumann, & Kobor, 2012; Gemma et al., 2013; Heyn et al., 2013), and this variability may be related to phenotype.

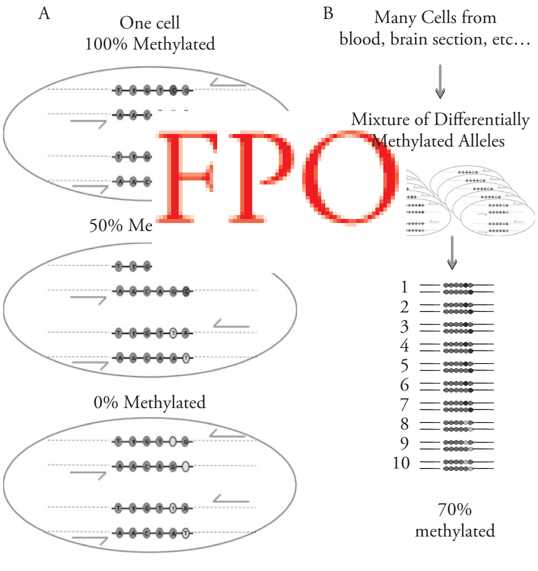

**Figure 20.2** Depiction of the derivation of methylation level from a single cell or tissue. (A) Single cells can be methylated at 100%, 50%, or 0%. Each allele in a single cell can be methylated, and this determines the percentage methylation of a single cell. Alleles are indicated by blue arrows, red circles indicate a methylated cytosine residue, and yellow circles indicate an unmethylated cytosine. (B) Tissues are made up of many cells. It is the combination of the methylation level from each cell that determines the overall percentage methylation of the tissue.

### *Individual Variability and Race*

A large-scale (~400,000 CpG sites) study of DNA methylation in individuals of African American, Caucasian American, and Han Chinese American descent was performed (Heyn et al. 2013). The level of methylation at a handful of sites (439 "population CpGs") was capable of distinguishing between geographic origin, indicating, not surprisingly, that epigenetic variability also exists between races and

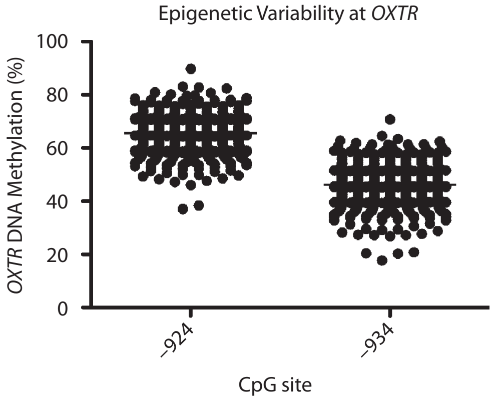

**Figure 20.3** Methylation of *OXTR* is variable among individuals. The methylation level of two CpG sites in the *OXTR* gene (–924 and –934) in the blood of 576 individuals is shown. Each dot represents the overall methylation for the indicated site in each individual.

may be important in describing the differences seen in phenotype between racial groups—a concept that was previously shown, although on a smaller scale (Fraser et al., 2012). Interestingly, although these epigenetic differences exist between groups, only 13 of the 101 promoter associated variants showed a relationship with gene expression, suggesting that the simple proposal that DNA methylation change must lead to gene expression change needs to be reconsidered. Other studies (Gemma et al., 2013; Kulis et al., 2012) have reported similar observations; Gemma and colleagues provide a thoughtful discussion of the implications of these results. Analysis of the epigenetic variation in the context of genotype found that two-thirds of the population CpG sites could be ascribed to differences in genetic variation, indicating the importance of considering underlying genetic background in studies of DNA methylation differences and the potential mediating/moderating effects of epigenotype on genotype–phenotype outcomes. One-third of the sites could not be ascribed to genetic variation, indicating that environmental or other unaccounted for mechanisms could affect phenotypic differences related to epigenotype. This important study lays the foundation for thoughtful work that may explain the range of phenotypic variability seen among geographically distinct populations.

### *The Stability of an Epiallele*

When considering the use of DNA methylation derived from blood in the study of phenotypic characteristics that are potentially related to an inherited or early established epigenetic variant, it is important to determine the stability of the epigenetic mark. The turnover rate of most blood cells is less than 1 month, being replenished at an established rate by hematopoietic progenitor cells. Gemma and colleagues tested the stability of established epialleles identified from CD14$^+$ cells isolated from blood over a 2- year period. Importantly, they verified the stability of these loci, indicating that the epiallele variability is likely established in the blood progenitor cells. Similar stability is also seen at the *OXTR* locus in DNA derived from a mix of lymphocytes and monocytes (peripheral blood mononuclear cells). Figure 20.4 shows the results of blood draw over a time period of 2½ years. Blood was isolated from a Caucasian female in her 30s, peripheral mononuclear cells were collected, and the DNA was extracted and subject to methylation analysis at site –934 in *OXTR*. Methylation level during the course of the 2½-year period did not differ significantly, and the variability in the measurement was within the established limits of the assay (±1.7%). These data point toward the ability to use this epi-allele in studies of phenotypic variability in similarly aged individuals.

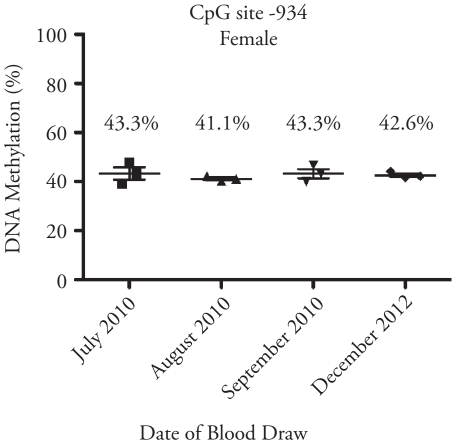

**Figure 20.4** DNA methylation level of *OXTR* is stable in blood. Overall methylation level of CpG site –934 was determined from DNA derived from peripheral blood mononuclear cells in a single individual during the course of 2½ years. Methylation levels indicate that this site is stably methylated in the blood.

## Epigenetics of Social Behavior

A potential role for epigenetic influences on social behavior has been a topic of recent interest across several areas of psychology and psychiatry. Traditional models in psychology have attempted to dichotomize the role of genetics and the environment on developmental and health outcomes—a framework that generally invokes debate about nature versus nurture. Until recently, *nature* was simply referred to as heritable traits without regard to the mechanisms by which genes may govern behavior. After the human genome was sequenced, nature began to be characterized by variability in the DNA with particular attention given to genes thought to be involved in core cognitive, affective, or social processes. Although this type of model is important for testing the influence of common, heritable genetic differences on phenotypic variability, we must acknowledge that reducing our level of *genetic* analysis to DNA sequence alone will be limited in two important ways. First, DNA sequence variability represents only one of many factors that may influence the function of the gene. Second, environmental factors have been demonstrated to impact the expression of genes without causing changes in DNA sequence. By holding the level of genetic analysis constant, we may not allow for inferences to be made regarding the mechanisms by which the environment may interact with the function of the genes and lead to variable behavioral and health outcomes. For these reasons, epigenetic mechanisms have been receiving increased attention for their potential role in complex behavior. Evidence for the role of epigenetics in typical and atypical social behavior derives from both animal models and association studies in humans.

### *Animal Models*

Early environmental factors have a tremendous influence on the development of an organism. For example, children growing up in poverty have a much higher incidence of cognitive and affective deficits, leading to low IQ scores, poor academic achievement, risky sexual behaviors, and poor health outcomes (Brooks-Gunn & Duncan, 1997; McLoyd, 1998). These outcomes are mediated by parental factors, such that those children who grow up in positive, nurturing environments are often buffered from the negative consequences associated with poverty (Miller et al., 2011). Although outcome is clearly tied to environment, the mechanisms by which parenting mediates the impact of poverty are less clear.

Animal models offer a unique way to address potential biological mechanisms that underlie variable outcomes. Unlike human studies, animal models allow researchers to systematically vary environmental factors and question how they may impact the function of genes. In the past decade, the past decade, it has been firmly established that a wide range of environmental influences, including but not limited to diet, exercise, and exposure to toxins, may alter gene expression and impact phenotypic variability (Jirtle & Skinner, 2007). Moreover, there is now evidence that an animal's social environment can impact epigenetic processes, leading to stable behavioral differences across the life span. A compelling example of this type of phenomena is illustrated in the seminal studies of Michael Meaney, Moshe Szyf and colleagues. In these studies, the researchers began with the observation that early maternal care in rodents directly influences the function of the hypothalamic–pituitary–adrenal (HPA) response to stress, and this influence lasts through adulthood. In this case, early experience directly programs a biological response that lasts across the life span. However, the exact biological mechanisms by which this programming occurs were elusive. By examining gene expression in the hippocampus of rodents, Meaney, Szyf, colleagues found higher levels of glucocorticoid receptors for those rodents reared in more nurturing environments (Weaver et al., 2004). Increased expression of glucocorticoid receptors in the hippocampus directly reduces the activity of the HPA response to stress, which helps to lessen the release of the stress-related hormone cortisol. Importantly, the relationship between environment and gene expression is directly mediated by DNA methylation. Specifically, the *NR3C1* gene that codes for the glucocorticoid receptor had higher levels of DNA methylation along the promoter region in the hippocampus of offspring raised in less nurturing environments. Methylation levels emerged early in development and remained stable across the life span (Weaver et al., 2004). These effects can be reversed via pharmacologically induced methylation changes to the gene, further suggesting a causal role for epigenetic mechanisms on gene expression changes in the hippocampus (Weaver et al., 2004; Weaver et al., 2005).

A similar relationship between early life stress and persistent changes in gene expression has been reported for the arginine vasopressin gene (*AVP*). Murgatroyd and colleagues induced stress in mouse pups by forcing a 3-hour separation from their mothers each day. This early life stress induces elevated *AVP* mRNA levels in the hypothalamus that are associated with hypomethylation of an enhancer region of *AVP* (Murgatroyd et al., 2009).

Early life stress has also been examined in nonhuman primates. More than five decades of research has established the importance of early life stressors associated with differential rearing in nonhuman primates. Classic work by Harry Harlow and colleagues has established that early social isolation in rhesus monkeys leads to a host of behavioral and physiological deficits (Harlow, Dodsworth, & Harlow, 1965), and the degree of social isolation may influence whether the effects may be reversed in adulthood (Harlow & Suomi, 1971). Provencal and colleagues (2012) tested whether the early life programming observed in these animals is mediated by an epigenetic mechanism. Specifically, the authors used similar rearing strategies as those used in the classical paradigm. The monkeys were divided into two groups: The first group of monkeys were raised by their biological mothers and socialized in a typical manner. The second group of monkeys were raised with an inanimate surrogate and had some opportunity for socialization with age-matched peers. Prior research has demonstrated that the latter group of monkeys often evince inadequate social skills, enhanced aggression, and typically rank lower in social dominance (Higley, Hasert, Suomi, & Linnoila, 1991). To address whether these deficits are due to epigenetic modifications, Provencal and colleagues compared DNA methylation, assessed from both the prefrontal cortex (PFC) and peripheral blood, across the genome for the two subject groups. The PFC was used as a central target given its known role in stress reduction and potential vulnerability to early stressful experience. The peripheral blood collection was included to test whether the epigenetic impact of early life experience was specific to neural regions governing stress behaviors or whether the impact could be observed systemwide. Indeed, the impact of the rearing process influenced DNA methylation at many sites across the genome. Moreover, this impact was not limited to the brain but could also be observed in peripheral blood. Although the majority of methylation changes were different for blood and brain, several areas of the genome showed promising overlap, which is consistent with the notion that the impact of early life stress on the epigenome may be systemwide and not limited to specific tissue types (Szyf & Bick, 2012).

Although many of the effects of early life social stress could lead to stable changes in both gene function and behavior, new research indicates that minor changes in social environment may be dynamically reflected in the expression of genes via DNA methylation. Tung and colleagues (2012) tested the impact of social status on gene regulatory variation in female macaques. Social hierarchy has previously been associated with stress and immune system function. Macaques living in the wild establish dominance hierarchies in which priority for food, water, and grooming partners is given to higher-ranking members. Whereas in the wild these dominance hierarchies rarely change, in captivity the dominance hierarchy is influenced by the order in which new animals are introduced to the group, with the newest member normally given the lowest status. Given the transient nature of the dominance hierarchy in captivity, Tung and colleagues tested for variation in gene regulatory systems as a function of experimentally induced social ranking. Dominance ranking was associated with variability in approximately 1000 genes—more than 100 of them specifically involved with the function of the immune system. Dominance rank was also associated with differences in DNA methylation, and genes that showed expression change were more likely to demonstrate variability in methylation. These findings offer a provocative hypothesis: Environmentally epigenetic modifications not only may function for extreme situations or developmentally critical periods but also may play a critical role in dynamic social environments.

The studies described previously strongly implicate epigenetic mechanisms as a biological link between early social experience and stable differences in behavior. The use of animal models allows for strict control over environmental influence and also provides opportunities for accessing tissue-specific change in key brain regions. Translating these findings to human development is a challenge. First, even in well-characterized human cohort studies, there are many systematic differences in early experience that cannot be easily controlled. Second, there is no easy way to noninvasively measure tissue-specific DNA methylation in the brain of a living human. This latter concern makes the findings from the nonhuman primate studies particularly compelling. If social experience can create systemwide changes to the epigenome, it is possible that in the future we may use peripheral tissues to make inferences about environmentally induced epigenetic modifications that underlie phenotypic variability.

### *Human Studies*

Although epigenetic processes are likely to be of major importance to complex behavior in both healthy and disordered populations, epigenetic association studies are just now beginning to be reported. A major issue facing epigenetic investigations in humans is tissue specificity of epigenetic modifications. Most behavioral epigenetic studies relevant to social behavior make inferences about gene regulatory systems that affect the function of the brain. Therefore, the tissue of interest is often neural tissue that is conventionally inaccessible for studies of humans. One potential solution to this problem is to take advantage of large postmortem data collections and tissue banks. Here, researchers may make inferences about environmentally induced epigenetic changes in neuronal function and how these differences could predict complex behavior or disease. Alternatively, studies in humans may examine peripheral tissues such as blood that may serve as a proxy for inaccessible brain tissue. In this case, it is important to note that there are several mechanisms that may lead to epigenetic variability, including but not limited to environmental impact, stochastic variability, and transgenerational inheritance.

Postmortem brain tissue studies offer a unique chance to translate results from animal models to humans. For example, consider the case of maternal care discussed previously in rodents, maternal care is associated with glucocorticoid expression in the hippocampus that has a direct impact on the function of the HPA response to stress (Murgatroyd et al., 2009; Weaver et al., 2004). This relationship is mediated via epigenetic mechanisms because poor maternal care is associated with higher degrees of methylation in the promoter region of the glucocorticoid receptor. McGowan and colleagues (2009) tested whether this relationship is also observable in humans. Specifically, they acquired hippocampal samples from a postmortem tissue bank of suicide victims and studied whether measures of early childhood adversity were predictive of differences in glucocorticoid gene function. They found evidence suggesting decreased gene expression in suicide victims with a history of abuse relative to those victims who had no history of abuse. Similar to the animal findings, decreases in gene expression were related to a higher degree of methylation along the promoter of the glucocorticoid receptor gene. Interestingly, they found no difference in gene expression or level of methylation for suicide victims with no history of abuse and controls, suggesting that this finding is indicative of the relationship between early life adversity and glucocorticoid receptor function and not necessarily related to other factors that may predict suicide.

Although postmortem studies allow for strong inferences to be made between epigenetic marks, gene expression, and neural function, the relative dearth of available tissue and appropriate phenotypic information pose a significant challenge to progress in the field. An alternative approach is to use peripheral blood as a tissue of interest when accessing epigenetic variability. The degree to which peripheral blood, or other accessible tissues such as saliva or germline cells, may predict phenotypic variability is currently under debate (Albert, 2010). New findings from cohort studies are offering promising results. For example, Borghol and colleagues (2012) acquired blood from 40 adult males belonging to the British Birth Cohort study and conducted a genomewide methylation analysis to determine whether early childhood socioeconomic status was associated with differential methylation. They found differences across the genome that were associated with early life socioeconomic status but not current socioeconomic status. Kobor and colleagues have established that demographic factors such as sex, age, race, and ethnicity are reflected in variability of methylation across the genome (Lam et al., 2012). Psychosocial factors, such as perceived stress and early life socioeconomic status, were also associated with DNA methylation. Unlike in the animal literature, however, DNA methylation found in this cohort study had little relation to gene expression in target genes. Although this relationship is often simplified and taken for granted, the work by Kobor and colleagues suggests that this is an avenue of research that deserves further clarification (Lam et al., 2012).

Human epigenetic studies may also investigate the role of transgenerational inheritance of *epimutations* and their role in phenotypic variability. Unlike environmentally induced epigenetic change, epimutations refer to modifications made to the genome that could be passed through the germline. Here, we would expect to find the epimutation present in all cell types, making peripheral tissues useful in epigenetic association studies (Labrie, Pai, & Petronis, 2012). However, caution must be exercised in the identification of epimutations because regions identified in a typical screen may have no causal role in complex behavior or disease. It is essential that target genes and regions of epigenetic variability be tested across relevant brain systems via postmortem studies or animal modeling via pharmaceutically induced epimutation.

Petronis and colleagues illustrated a role for germline epimutations in complex disease. The authors tested the association between bipolar disorder and DNA methylation of *HCG9*, a gene previously associated with psychosis (Purcell et al., 2009). In a large sample of patients with bipolar disorder, Kaminsky et al. (2011) demonstrated lower methylation of *HCG9* from three different tissues, including PFC from postmortem tissue and sperm cells and peripheral blood from a living sample. Although it is impossible to build a causal model for disease from this association study, the inclusion of three different tissue types helps to establish evidence of an epimutation that may be considered a heritable risk factor. Perhaps more important for human studies, this work provides evidence that accessible tissues such as germline cells and peripheral blood may be relevant for understanding complex behavior and disease.

Epigenetic variability is also thought to play a critical role in autism spectrum disorders (ASD), which are characterized by deficits in normal social functioning. Early investigation of epigenetic mechanisms in ASD focused on genomic imprinting, a process by which a gene may be silenced via epigenetic mechanisms or via mutation of genes that play a role in epigenetic regulation (Samaco, 2004; Schanen, 2006). Methylation differences along genes suspected to be involved in ASD phenotype have been proposed. Gregory, Connelly, and colleagues (2009) tested for differences in gene expression and DNA methylation of the oxytocin receptor gene (*OXTR*) in ASD. Oxytocin (OXT) is a nonapeptide hormone whose action has been demonstrated to play an important role in a variety of social processes and is often hypothesized to play a role in social deficits in ASD. In humans, the actions of OXT are mediated by a receptor that is encoded by *OXTR* (Kimura, Tanizawa, Mori, Brownstein, & Okayama, 1992). Gregory, Connelly, et al. analyzed a region of the promoter of *OXTR* that had previously been associated with DNA methylation-induced gene expression changes (Kusui et al., 2001) and found an association between methylation and the presence of ASD in postmortem brain tissue from individuals with ASD. Of note, increased methylation in this site was linked to decreased *OXTR* transcription in temporal cortex regions believed to be important for social cognition (Pelphrey, Adolphs, & Morris, 2004; Pelphrey & Morris, 2006; Puce, Allison, Bentin, Gore, & McCarthy, 1998). Moreover, the authors also found a similar pattern of increased methylation of *OXTR* in peripheral blood for those with ASD relative to controls (Gregory, Connelly, et al., 2009).

## Epigenetics and Human Neuroscience

Traditional studies in behavioral genetics have been conducted in the absence of information regarding the function of particular genes. In these studies, investigators focus on heritability of complex traits or behaviors while attempting to control for the influence of the environment. With the sequencing of the human genome, genetic association studies have attempted to link heritability with variance in the DNA sequence. Human neuroscience techniques such as functional magnetic resonance imaging (fMRI) have benefited from these association studies because they have provided unique ways to define phenotypic variability and link the function of a gene with a particular biological process. Here, we review the strengths of contemporary approaches in imaging genetics and discuss how consideration of epigenetic factors may advance the field.

### *Functional Genomics*

Contemporary approaches linking genetic variability with typical and atypical social behaviors focus on common genetic polymorphisms in candidate genes. A genetic polymorphism refers to sequences within a gene that show common variation in the population. There are several different kinds of polymorphisms that may describe variable sequences of nucleotides within the gene. To date, most research has focused on single nucleotide polymorphisms (SNPs), a region of the genome that varies at one nucleotide in comparison to the reference genome. SNPs may occur at any part of the gene, including portions of the gene that influence transcription and lead to variable production of mRNA and protein. Variability at the molecular level, as measured by SNPs, may have an impact on gene function and therefore could influence the phenotype. However, although techniques now allow for the mapping of the entire human genome, relationships between SNPs and complex human behavior have been limited. These limitations are likely due to the phenotypic definition afforded by descriptions of complex behavior. Complex behaviors are often measured as constructs dependent on observable traits or self-reports. The gap between levels of measurement of molecular genetic variability and behavioral reports is thought to be an impediment to drawing meaningful gene/behavior associations. This limitation is common in behavioral genetics and has led investigators to identify reliable endophenotypes—an intermediate phenotypic measurement that may be more closely related to the operation of the gene (Gottesman & Gould, 2003). In imaging genetics, researchers use quantifiable differences in blood oxygen level-dependent (BOLD) activity from brain regions that are thought to underlie complex behaviors. These regions may often be identified in simple perceptual and cognitive tasks, and the variability in activity is often indicative of individual behavioral differences. Current studies in "imaging genetics" focus almost exclusively on SNPs that can be found in an array of candidate genes supporting various social and cognitive functions. In these studies, individuals are characterized by either the presence or the absence of a particular allele type and grouped accordingly. Activity from candidate brain regions is quantified for each group, and differences are assessed.

To illustrate the approach of imaging genetics, let's consider the role of common genetic variants in the serotonin system and their potential impact on social behavior. Serotonin is powerfully implicated in human social behavior and mental health. Serotonergic responses are governed by the 5-HT transporter (5-HTT) that is encoded by a single gene (*SLC6A4*). Lesch and colleagues (1996) first reported that a polymorphism in the promoter region impacts gene transcription and is associated with anxiety disorders. These allele types are described as long (ls) and short (ss) given that they impact the length of a repeat element in the promoter. Specifically, carriers of the short allele exhibit decreased 5-HTT expression and are more likely to report anxiety-related personality traits. In a seminal study, Hariri and colleagues (Hariri, 2002) found that carriers of the short allele show greater amygdala reactivity when viewing facial expressions of emotion relative to those who are homozygous for the long allele. This report is important for several reasons. First, it provides a direct link between gene variability and brain systems underlying social perceptual processing. Second, by using amygdala activity as a dependent measure, the authors were able to show significant differences between groups with only 28 subjects, and the effect size was more than six times greater than that of the original association studies by Lesch and colleagues. Finally, it demonstrates how variability in perception, as assayed by amygdala activation, is related to both genetic predisposition at the molecular level and stable personality traits at the phenotypic level. Imaging genetics approaches have become quite common during the past decade and often include measures of both function (fMRI) and structure.

### *Limitations of Contemporary Approaches*

Although current approaches in imaging genetics have been a major advance in gene/behavior associations, there are limitations both biologically and statistically that may be addressed through complimentary lines of research. On a biological level, identified markers, or variants, should not only be predictive of a phenotype or an endophenotype but also allow for generation of obvious hypotheses about changes in gene function. For the vast majority of SNPs that have been implicated in human phenotypes, no known function has been described or is obvious. Moreover, this approach forces us to dichotomize our groups by allele type while ignoring significant variability within groups. Finally, allele frequencies often vary across race and ethnicity, and for some particular variants, it is difficult to find large enough samples of particular allele carriers. Such limitations may be addressed, at least in part, by consideration of epigenetic processes. Inclusion of epigenetic information will advance imaging genetics approaches in two critical ways. First, epigenetic modifications often have a direct impact on gene expression, and models of gene function can often be verified with molecular studies (Kusui et al., 2001). Second, continuous measures such as DNA methylation are better suited for statistical analysis in functional neuroimaging studies. Specifically, statistical power will be increased based on the unit of measurement. Contemporary SNP studies are forced to dichotomize the groups and test for differences in the function of candidate brain regions between groups. After isolating DNA, investigators divide their subjects into two separate groups, and then try to determine whether regional brain activity, averaged from subjects within each group, is statistically different between groups. Although fMRI has the statistical power to allow for between-group analyses, the design is inherently less powerful than a within-group design. In this approach, the degree of DNA methylation may be assessed in a given sample; this is an indication of both the number of cells that are methylated in that sample and the methylation state inside a single cell (no alleles, one allele, or both alleles methylated). For each individual, a single metric may represent the methylation status of a particular genomic region. This metric can then be correlated with individual variability in brain activity in a social/cognitive task. Using a unit of genetic analysis that is represented with a continuous variable will allow for more statistical power, allowing identification of changes with small effect sizes without requiring the large sample size necessary for conventional polymorphic analyses. Furthermore, this approach allows for a fine-grained appreciation of individual differences.

Finally, the epigenetic approach is a natural complement to the more contemporary SNP approach. What is the relationship between genetic polymorphisms and epigenetic modifications on the same candidate gene? Under what circumstances would transcript information, SNP information, or interaction of the two better predict structural or functional brain differences? Consideration of the role of epigenetic modifications on phenotype will allow for more accurate models of genotype/phenotype relationship and promote better understanding of typical and atypical behavior. We propose a basic model whereby typical brain function varies on a continuum that can be partially accounted for by the functional DNA methylation pattern of a gene (or group of genes) and that disease associated within the brain lies on each end of this spectrum (Figure 20.5). We argue that epigenetically regulated regions are likely to contribute to neuroregulatory systems that govern social behavior and are influenced by social experience.

Epigenetic neuroimaging studies are just now beginning to take shape. In our laboratories, we have begun testing the feasibility of the approach with a well-characterized epigenetic modification on the oxytocin receptor gene. As previously mentioned, Gregory, Connelly and colleagues (2009) established that increased *OXTR* methylation was linked to decreased expression in temporal cortex and was associated with the ASD phenotype. Moreover, peripheral blood from living humans showed the same pattern of association, making it a particularly attractive candidate gene for an imaging epigenetic study. Given the evidence suggesting OXT's role in social perception and *OXTR* methylation-related transcription differences in temporal cortex of persons with ASD, we hypothesized that *OXTR* methylation would be particularly predictive of functional differences near the temporoparietal junction.

To assess this prediction, we utilized a classic social perception task first developed by Heider and Simmel and later adapted by Castelli, Happé, Frith, and Frith (2000) in which simple geometric shapes move in ways that imply either social interaction (animate motion) or random motion. Although subjects do not always receive specific instructions when viewing the displays, the animations often spur descriptions of causality and "social intent" for the displays that depict animate motion. Imaging studies have indicated that these "animate" videos activate a network of structures important for social perception, including the temporoparietal junction.

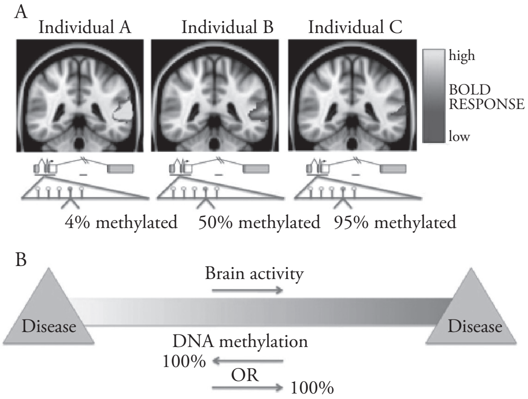

**Figure 20.5** A fictional model of normal variation in brain response to social stimuli explained by epigenetic variation. (A) Individual differences in response to social stimuli are seen, as measured by change in blood flow (BOLD response). These individual differences correlate with the degree of DNA methylation of a specific locus. (B) Normal brain function varies on a continuum that can be partially accounted for by the DNA methylation level of each individual's genome. Disease states lie at the ends of these continua.

To test the hypothesis that *OXTR* methylation was related to temporal lobe function during social perception, 43 healthy volunteers submitted blood samples and then participated in our perception of animacy paradigm. Whole-brain analysis indicated that the degree of *OXTR* methylation was significantly associated with BOLD activity in the Animate > Random contrast in clusters in the left superior temporal sulcus (STS) and the dorsal anterior cingulate cortex. Specifically, individuals with higher levels of *OXTR* methylation demonstrated greater activity in these regions. The region of the temporoparietal junction was close to the area that previously showed a relationship between increased *OXTR* methylation, reduced *OXTR* expression, and ASD phenotype in postmortem brain tissue. The same region has also been identified in imaging studies to be sensitive to the degree to which subjects attend to social contingencies (Blakemore et al., 2003) or attributions of causality (Morris, Pelphrey, & McCarthy, 2008).

We also genotyped each participant for two SNPs, rs2254298 (G>A) and rs53576 (G>A), previously associated with variability in a wide range of social behaviors (Jacob et al., 2007; Rodrigues, Saslow, Garcia, John, & Keltner, 2009; Tost et al., 2010). Whole-brain analysis identified significant interactions between *OXTR* methylation and SNP rs2254298 genotype in predicting Animate > Random activity in left STS and right temporal pole. Here, individuals were dichotomized into groups based on whether they were homozygous G carriers (GG) or whether they possessed an A allele (AA). Post hoc probing of these effects indicated that methylation predicted left STS activity for GGs but not AGs. Similarly, *OXTR* methylation predicted right temporal pole activity for GGs but not AGs. GGs with higher methylation demonstrated greater Animate > Random activity in both these regions (unpublished data).

Results of this initial investigation powerfully implicate DNA methylation of *OXTR* in explaining variability in neural systems supporting social perception. Remarkably, this effect appears to operate in an allele-specific manner, whereby the effects of DNA methylation appear much greater for individuals of a particular genotype. The brain regions displaying significant associations with methylation and genotype showed distinct overlap with sites previously identified as playing a key role in mentalizing processes, namely STS, temporal poles, and medial prefrontal regions. In general, individuals with increased risk in a variety of forms (i.e., GG individuals and/or individuals with higher *OXTR* methylation) showed greater activity in these regions when viewing animate versus random movement. We interpret such activity as indicating more resource-intensive processing. Activity in STS, for example, has previously been found to increase in situations in which more elaborated processing of moving social stimuli is required, such as when a character's actions are incongruent with expectations (Pelphrey, Morris, & McCarthy, 2004; Pelphrey, Singerman, Allison, & McCarthy, 2003).

Collectively, our findings suggest that individuals with higher degrees of *OXTR* methylation, particularly those with the risk (G) allele, both expend more initial effort in social attribution processes and continue to invest more resources in these processes over time. This provides the first extant demonstration of a potential mechanism by which *OXTR* methylation is impacting the behavioral phenotype. However, it is notable that all individuals in this study were neurologically and psychologically healthy. Therefore, it is possible that while *OXTR* methylation is clearly impacting brain systems supporting social perception, other factors may enable those high in methylation to remain resilient to disordered social behavior. Alternatively, this relationship between *OXTR* methylation and neural systems supporting social perception may be predictive of more complex social phenotypes.

A second imaging genetics study has explored the role of DNA methylation of the catechol-*O*-methyltransferase (*COMT*) gene on stress and PFC function in a cohort of subjects with variable life stress. The enzyme COMT degrades dopamine in the human brain. A functional SNP along the *COMT* gene contains a G→A polymorphism that results in an amino acid change from valine to methionine. Carriers of the G or Val allele demonstrate greater enzyme activity that has been associated with a blunted stress response and less efficiency in the PFC during cognition (Egan et al., 2001; Mier, Kirsch, & Meyer-Lindenberg, 2010). Notably, the Val allele type creates a CpG dinucleotide, making methylation possible, whereas carriers of the Met allele do not have methylation along this string of DNA. Ursini and colleagues (2011) demonstrated that homozygous Val carriers had a significant relationship between DNA methylation and lifetime stress. Specifically, lower methylation values were associated with higher rates of lifetime stress as measured by self-report. Moreover, methylation interacts with lifetime stress to modulate prefrontal activity during working memory, such that low stress and high methylation lead to greater prefrontal efficiency. Although the relationship between *COMT* methylation in peripheral blood and PFC is unknown, Urisini and colleagues also demonstrated that *COMT* methylation is correlated in the blood and brain of rats, allowing for the potential for this epigenetic mark to be used as a biomarker in human cohorts.

Both our study and that of Urisini and colleagues have several limitations that need to be addressed in future research. First, both studies relied on peripheral blood mononuclear cells as the source of epigenetic analysis. DNA methylation is a tissue-specific phenomenon, and the degree of methylation could be much different between blood and brain for a great deal of CpG sites along the genome. This limitation is tempered by the fact that both studies report secondary data suggesting similar patterns between blood and brain. For example, the *OXTR* target was chosen because it was first found to be predictive of ASD in both postmortem temporal lobe tissue and peripheral blood, whereas the *COMT* target demonstrated a correlation between brain and blood in a rodent model. Future studies should continue to validate epigenetic targets molecularly, via postmortem tissue, or with animal models. A second limitation of these studies is that the conclusions are limited to psychologically and physically healthy adults. Future research should consider the impact of epigenetic variability both across the life span and within the context of developmental and psychiatric disorders. Third, the nature of the variability is unknown. Although it is tempting to speculate that the *COMT* methylation is related to early life experience, or stress, the directionality of the relationship between the two cannot be determined. For example, stochastic or heritable epimutations could also lead to methylation differences, and perhaps these methylation differences have an impact on phenotypic variability. The source of variability for particular epigenetic targets needs to be established with complimentary lines of research that focus on molecular and developmental trajectories. Finally, as in all imaging genetic studies, it will be important to establish how the relationship between epigenetic variability and brain activation impacts differences in overt behavior in both typical and disordered populations. This limitation can be addressed with vigorous behavioral testing or by making use of human cohorts that have been rigorously tested on particular psychological constructs.

### Future Directions and Implications for Cultural Neuroscience and Health Disparity Research

The Human Genome Project was a $3 billion initiative that took approximately 13 years to complete. Studies immediately began to test the influence of particular common genetic variants on a host of complex behavior and disease. Indeed, new technologies allowed researchers to move past specific genetic targets and access the role of the entire genome on phenotypic diversity. These techniques, referred to as genome-wide association studies, allow researchers to affordably consider the role of SNPs as markers of genetic diversity and in turn assess how they may predict behaviors or disease of interest. Although many had hoped that these technologies would provide a causative link between specific genes and specific traits that are concordant with known heritability estimates, these types of findings have not occurred. The influence of any one SNP on a heritable behavior is generally less than 1% of the total variance (Turkheimer, 2011). Even considering the role of all possible variants on highly heritable traits leaves one with very little predictive ability. The gap between heritability and genetic explanation has been referred to as the "missing heritability problem" (Maher, 2008), and it has caused criticism of a reductionist approach and even some calls to ditch genetic explanations in favor of a strict ecological approach to complex traits (Joseph, 2012). In this chapter, we have highlighted how epigenetic factors may influence gene expression and be related to phenotypic variability. Moreover, we have illustrated how epigenetic factors may lie at the intersection between environmental influences and biological processes. Although consideration of epigenetic phenomena will not solve the missing heritability problem, it will expand our understanding of the relationship between genes and behavior, and it might be especially critical when considering the interaction of genes and culture.

Culture–gene coevolutionary theory suggests that cultural values are subject to the same physical, social, and environmental pressures that may influence genetic selection. Chiao and Blizinsky (2010) offered a compelling example of culture–gene coevolution and social behavior. Here, the authors suggest that historical levels of pathogen prevalence may impact the degree of collectivism in a culture and that this pressure may have placed pressure on genetic selection. Specifically, they tested the association between collectivism and allelic frequency of the serotonin transporter functional polymorphism. As mentioned previously, the short allele type (S) has been previously associated with higher risk of anxiety disorders and great amygdala reactivity during social perception. Chiao and Blizinsky found that collectivistic cultures were more likely to be composed of individuals carrying the short allele relative to individualistic culture. Highly collectivistic cultures could have offered protection from the probability of environmental stress associated with pathogen prevalence, which could explain both the higher rates of short allele carriers and the buffering effects of collectivism on the prevalence of anxiety disorders in individuals who live in collectivistic societies. Unfortunately, it is difficult to track changes in cultural norms based on differences in sorting and selection of DNA sequence. The timescale of natural selection is long, and definitive proof for these types of changes is a challenge for human populations. On the other hand, transgenerational epigenetic changes may also impact phenotypic variability and changes may occur much quicker than typically imagined under traditional Darwinian evolution (Nätt et al., 2012). Epigenetic studies may also allow us to test the influence of common environmental pressures on environmentally influenced epigenetic changes. By tracking these changes, we can then ask how environments may influence gene function and subsequently lead to cultural differences in complex behaviors.

Cultural neuroscience is a relatively new field of inquiry that integrates techniques from several disciplines, including cultural psychology, genomics, and human neuroscience. Currently, the role of epigenetic influences on cultural diversity is poorly understood. Given the natural links between environment and biological function, epigenetic processes are poised to play a critical role in new approaches to understanding the biological underpinnings of culture.

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CHAPTER

# 21

# The Encultured Genome: Molecular Evidence for Recent Divergent Evolution in Human Neurotransmitter Genes

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**Abstract**

This chapter aims to stipulate a line of research on the role of culture in recent human evolution. We discuss and evaluate several common arguments against recent human evolution. Second, we summarize empirical evidence for recent human evolution from classic examples to recent genome-wide searches. Third, using three data sets, we present detailed analyses of the extent of universal and group-specific selection of genes that are most relevant to human behaviors, namely neurotransmitter genes. We found that (1) a large number of neurotransmitter genes expressed in the central nervous system showed evidence of recent selection; (2) approximately one-fourth of these selection events appeared to be common among the four groups studied (i.e., Africans, Europeans, East Asians, and Australian Aborigines); and (3) selected gene variants were generally associated with better school-related skills but poorer performance on some cognitive and socioemotional traits, which seemed consistent with the human self-domestication hypothesis.

**Key Words:** evolution, natural selection, human genome, culture, neurotransmitter genes

A typical discussion of human evolution is about the evolution *to* humans—that is, how 4 billion years of biological evolution went from single-celled organisms living in the primordial soup to a small branch labeled *Homo sapiens* among approximately 9 million such branches in the tree of life (Mora, Tittensor, Adl, Simpson, & Worm, 2011). Knowing the evolutionary past of our species helps us to understand many of our biological and social processes that are shared with various other life forms (from sensory functions to sexual reproduction strategies) as well as the processes that are not shared with other life forms (i.e., species-specific traits such as bipedalism and speech).

However, in order to fully understand how evolution has shaped human behaviors, we also need to consider the evolution *of* humans (i.e., the continuing evolution since *H. sapiens* appeared approximately 200,000 year ago). Specifically, we need to understand (1) species-wide directional selection or balanced selection since the time of speciation and (2) group- or environment-specific selection after dispersal (i.e., after *H. sapiens* moved out of Africa and spread throughout the world). These changes over time and their variations across groups should reflect the varying evolutionary selection pressures as a result of adaption to different physical (pathogens, climates, etc.) and sociocultural environments (lifestyles, diets, social relations, etc.). In other words, we need to understand how ecological and cultural changes and variations might have contributed to the current human genome(s). Such research is an integral part of cultural neuroscience (Chiao, 2009, 2011; Chiao & Ambady, 2007). Until very recently, however, little attention has been paid to these two types of evolutionary processes, perhaps due to both academic and political reasons. Research on these processes, however, is essential not only for us to better understand the recent evolutionary history of our species but also for us to discover whether recent evolutionary history would explain why certain individuals and groups are more vulnerable than others to certain diseases and disorders.

In this chapter, we focus on the evolution *of* humans, particularly on genes that are most relevant to human behaviors, namely neurotransmitter genes. First, we discuss and evaluate several common arguments against evolution *of* humans (or recent human evolution). Second, we summarize empirical evidence for recent human evolution from classic examples to recent genome-wide searches. Third, we present detailed analyses of neurotransmitter genes based on three sets of data to show the extent of universal and group-specific selection, both of which should be informative to our understanding of the role of culture in human brain functions. Finally, we discuss directions for future research, implications for cultural neuroscience, and relevant issues in studying group differences in recent human evolution as well as their implications to the discussion about population health.

## Typical Arguments Against Recent Evolution of Humans

Researchers have argued against evolution *of* humans for both academic and political reasons. Academically, disciplines such as evolutionary psychology or its predecessor, “sociobiology,” want to emphasize the continuity between the animal kingdom and humans, so they would like to make claims such as “Our modern skulls house a Stone Age mind” (Cosmides & Tooby, 1997). Two prominent evolutionary psychologists, John Tooby and Leda Cosmides, once declared that the structure of the mind “reflects completed rather than ongoing selection” (Tooby & Cosmides, 1990. p. 381). Their main argument is that evolution is an extremely slow process and there simply has not been enough time since the Pleistocene for modern humans to continue to evolve. Within that framework, much of evolutionary psychology has focused not on how human behaviors have evolved since the Pleistocene but, rather, on the behavioral patterns we share with our Stone Age ancestors, other primates, and even more distant animal relatives. Based on that perspective, human universals are “evolutionary,” but all human variations are cultural. Therefore, this discipline seemed mainly interested in studying human universals (e.g., mating strategies, aggression, and basic social interactions such as kin recognition and cheater detection) (Buss, 2005).

Indeed, evolution can be a very slow process: It took 3.5 billion years for life to evolve from single-celled to multicellular organisms. But does evolution *have to* be slow? The answer is no. Fossil records show that a large number of new life forms can appear in a blink of an eye (in an evolutionary timescale)—for example, “the Cambrian explosion” (which accounts for the emergence of most animal phyla, accompanied by similar explosive speciation in land plants), which is believed to be driven by the convergence of various environmental (e.g., oxygen levels), ecological (e.g., food chains), and biological (e.g., crossing a threshold in genetic complexity) factors (e.g., Marshall, 2006). On a smaller timescale, a few thousand years of dog breeding have created dogs as diverse as 4-inch-long Chihuahuas and 7-foot-long Great Danes (for the dog genome, see Lindblad-Toh et al., 2005). In other words, when there is enough selection pressure, evolution can occur very rapidly. Theoretically, even if the selection pressure is modest (i.e., the advantageous allele has only 5% more offspring than the less advantageous allele), it takes only 200 generations (or 4000–5000 years for humans) for a new dominant mutation to reach near fixation (Jobling, Hurles, & Tyler-Smith, 2004) (Figure 21.1).

The second argument against recent human evolution is that once humans invented culture, natural selection was halted because humans could “overcome” nature through culture. For example, the invention of clothing made it unnecessary to evolve (or regress to) thick fur even in cold climates. The invention of tools and weapons made it unnecessary to increase physical strength and brute force in the competition for survival. Seeing the power of culture (the evidence for which is all around us), some happily declared, “Evolution is over. Things have simply stopped getting better, or worse, for our species” and “I don’t think we are going to see any changes [in humans]” (Jones & Ward, 2002).

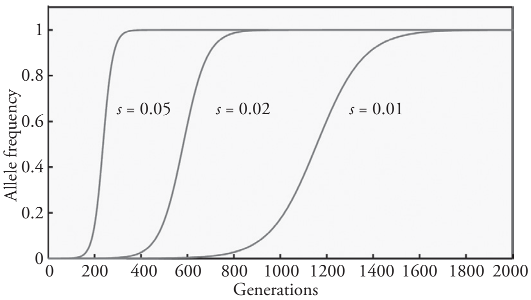

**Figure 21.1** Positive selection for an advantageous allele.
Source: Based on Figure 5.11 in Jobling et al. (2004).

Indeed, the co-discoverer of natural selection, Alfred Russell Wallace (1864), already noted that the development of culture allowed humans to inhabit regions without biological adaptation (for example clothing allowing inhabiting cold regions). Thus natural selection no longer plays a role in the evolution of the body.

The argument for culture replacing natural selection sounds intuitive, but it suffers the fallacy of separating humans from nature (environment). Humans are part of nature, and whatever humans create, call it culture or by any other name, becomes part of their environment. Indeed, for humans, culture has "become" their environment. Perhaps the invention of tools and weapons stopped human evolution toward having a more robust physique, but the use of tools and weapons has most likely put pressure on selection based on the skills related to tool use. If such skills have more to do with the mind than the body, culture indeed is the new selection agent. In fact, after acknowledging the role of culture in halting the evolution of the human body, Alfred Russell Wallace claimed that natural selection solely exerts its effects on human mental and moral attributes (Wallace, 1864). "Man's *body* will have remained generically, or even specifically, the same, while his *head* and *brain* alone will have undergone modification." (Wallace, 1864, italics in the original). Charles Darwin also concurred in a letter to Wallace, "The great leading idea is quite new to me, viz. that during late ages the mind will have been modified more than the body" (Darwin, 1864). Therefore, in later sections, we specifically focus on the genes related to the mind—neurotransmitter genes.

An auxiliary argument in pitting culture against nature is that anything that is not in the "natural" environment is irrelevant to evolution because natural selection works only on things in "nature." Typifying such a view in the popular media, Marilyn vos Savant (a columnist for *Parade* magazine who is known for being named as having the "highest IQ" in the late 1980s in the *Guinness Book of World Records*) wrote (vos Savant, 2013),

> Cigarettes don't exist in nature, so our genes don't carry any information about smoking. The same with alcohol: It's not a natural drink for any animal (and is rarely found in nature), so no one is programmed to be unable to stop drinking alcohol. (p. 5)

Although it is true that evolution cannot work without "raw materials" (in this case, genetic mutations relevant to human-made products), it is worth noting that (1) many human-made products have natural elements, including nicotine and alcohol, that have been found even in outer space (Charnley, Kress, Tielens, & Millar, 1995), and there are relevant biological processes to metabolize them; and (2) biological entities are versatile in accommodating new elements (thus, substance addiction to many new, synthesized chemical compounds). Furthermore, humans have been making alcohol since 10,000 bc (Patrick, 1952) and chewing or smoking tobacco since 1400 bc (Goodman, 2005). Consequently, not only are there alcohol dehydrogenase genes and nicotine receptor genes but also they have had ample time to experience "cultural" selection for variants that tolerate/modulate consumption.

The third argument typically relies on a numbers game. It is often said that humans are a young species and hence are genetically 99.9% alike. With such near-complete homogeneity in the human genome, certainly there is no room for the recent evolution *of* humans. However, to put the magnitude of that difference in context, the chimp and human genomes are 98.5% alike using the same method of estimation (single nucleotide substitutions) (Mikkelsen et al., 2005). With 99.9% identity, given that the human genome has 3 billion base pairs, 0.1% of the genome means 3 million differences (Abecasis et al., 2010, 2012; International HapMap Consortium, 2007).

Furthermore, the 99.9% similarity is an overestimate because it is based on single nucleotide polymorphisms (SNPs), and DNA variation also consists of insertions/deletions, copy number variations, inverted repeats, etc. For example, the Database of Genomic Variants (http://dgv.tcag.ca/dgv/app/home) shows that humans are only 99% alike or 1% different when all DNA changes are accounted for (the comparable number for human–chimpanzee differences is approximately 3% or 4%; Abecasis et al., 2012; Varki & Altheide, 2005).

The fourth argument is that even if humans differ in their genomes, such differences are inconsequential to their behaviors and traits. Much of this argument derives from the neutral theory of molecular evolution. According to this theory, "at the molecular level evolutionary changes and polymorphisms are mainly due to mutations that are nearly enough neutral with respect to natural selection that their behavior and fate are mainly determined by mutation and random drift" (Kimura, 1983, p. xii). Although the neutral theory has dominated the field for decades, it has begun to yield toward a compromise in the neutralist–selectionist debate. Kimura's student, Tomoko Ohta, re-emphasized the key word "nearly" in Kimura's original statement and proposed the "nearly neutral theory" (Ohta, 2002). Of course, the neutralist–selectionist debate was mostly about life forms in general and rarely about humans. When it comes to human evolution, the neutral hypothesis has not been challenged. Until very recently, the only accepted belief was that any variations in the human genome are due to genetic drift, not natural selection. With the neutralist–selectionist debate shifting toward a compromise, the debate should no longer be about whether evolution stopped for humans but, rather, about the extent of recent evolution of humans. The task now is to distinguish between the (likely many) neutral polymorphisms and the (likely few) selected variants.

Finally, researchers have been reluctant to talk about recent human evolution perhaps because human genetics has had a perilous history and it has carried the shadow of eugenics for the past century (Kevles, 1985). Declaring a biological, evolutionary, or genetic basis for human behavior has been labeled as biological determinism. When the behavior in question involves value judgment (intelligence, morality, aggression, or even a proxy such as brain size, etc.), research on its genetic basis is deemed as politically dangerous or even racist. As Steven Pinker was quoted saying, "People, including me, would rather believe that significant human biological evolution stopped between 50,000 and 100,000 years ago, which would ensure that racial and ethnic groups are biologically equivalent" (McAuliffe, 2009, p. 58). His careful choice of words is interesting: He was talking about a belief rather than a scientific statement, and he was limiting his belief to "significant" biological evolution.

In summary, there have been both academic reasons and political concerns behind the reluctance in examining recent human evolution. These reasons and concerns, however, may have been overstated or misconstrued. Just as knowing that Earth is not the center of the universe did not take away our awe for its magnificence and knowing that we descended from "monkeys" did not take away our dignity, knowing that humans have recently evolved and different groups may have experienced differential evolution should not take away our admiration for life's diversity. Instead, as C. P. Snow (1964) commented on the fear of studying the brain and human nature, "No one can predict what such an intellectual revolution will mean: But I believe that one of the consequences will be to make us feel not less but more responsible towards our brother men" (p. 75). His comment can be equally applied to the study of genetic diversity among humans. Biological species need diversity for survival. Ending his *On the Origins of Species*, Charles Darwin (1998) wrote, "[F]rom so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved." (p. 649). Admiring the evolution of life's endless forms, Darwin specifically added "are being" to emphasize the continuousness of the process. He did not make an exception for humans.

## Evidence for Recent Human Evolution

By countering the prevalent arguments against recent human evolution, the previous discussion pointed to the possibility (or theoretical inevitability) that humans must have evolved recently and are still evolving. What is then the evidence for either recent species-wide or group-specific selection? First, we present a few classic examples. These are well-documented examples and have been strengthened with increasing empirical evidence. By briefly examining these examples, we can learn a few important lessons about human evolution in general.

### *Classic Examples of Recent Human Evolution*

The first example is skin color. Given its visibility and stability as well as its importance in human grouping, researchers have systematically examined the mechanisms involved in this group-specific evolution (for an extensive discussion, see Jablonski, 2006; Jablonski & Chaplin, 2010). It was found that when humans expanded to higher latitudes, they would have experienced reduced sunlight (ultraviolet (UV)) exposure (perhaps further impacted by the invention of clothing, which was needed to survive the cold climate). In that environment, a lighter skin would have the advantage of taking in more UV, which is needed for the human body to produce vitamin D. Recent research (e.g., Lao, de Gruijter, van Duijn, Navarro, & Kayser, 2007; Sturm, 2009) shows that this evolutionary process involved a number of genes: *MC1R, ASIP, ATTRN, DCT, KITLG, OCA2, SLC24A5, SLC45A2,* and *TYR.* The second well-documented example of recent group-specific human evolution concerns malaria resistance, which is a century-old topic. Recent research (e.g., Hedrick, 2011; Piel et al., 2010) has shown that independent hemoglobin mutations such as *HbC* and *HbE*, as well as mutations in other genes such as *G6PD, DARC,* and *MHC*, have been involved in human evolution's fight against malaria. These mutations, by definition, are predominantly found in human populations susceptible to malaria. Finally, lactase persistence (lactose tolerance) is another example of recent group-specific human evolution. At least four independent mutations for lactose tolerance near the lactase gene (*LCT*) have been identified (Tishkoff et al., 2007), with some variants having very recent origins (e.g., 3000 years ago). Only human populations that domesticated cattle and drank their milk as adults show evidence of selection for these variants.

Three main lessons can be learned from these three classic examples. First, evolution in humans can be *rapid.* Gene variants for malaria resistance and lactase persistence are as young as 3000 years old. Second, due to the selection pressure, evolution is relentless and would work on multiple loci throughout the genome, resulting in s*eparate* selection events for the same evolutionary advantage (or convergent evolution; Pritchard, Pickrell, & Coop, 2010). These selection events can be separate events for different genes but also separate events for the same gene—for example, the appearance of lactase persistence variants in Europe and the Middle East at approximately 4000 BC and a more recent (as recent as 1000 BC) mutation in East Africa. Third, the selection of lactase persistence is notable because it was directly driven by a human-made/*cultural* environment (i.e., animal domestication and milk consumption).

Although these examples have helped shift the selectionist–neutralist debate and have important implications for the evolution of other human traits (and associated genes), their significance is limited if the near neutralists are correct, namely these examples represent exceptions rather than the norm. What is the extent, then, of natural selection in recent human history?

### *Genomic Evidence for Recent Evolution*

With the availability of increasing genomic data since the completion of the Human Genome Project, the field of molecular evolution began to discover, to the disbelief of many, that not only is there strong evidence of recent human evolution but also it was extensive and very recent. Early 2006 marked the year when two independent labs published genome-wide searches for evidence of positive selection in the human genome. Wang, Kodama, Baldi, and Moyzis (2006) used data from two sources (HapMap and Perlegen) to systematically document signatures of recent positive selection in the whole genome. They found that approximately 1800 genes showed strong signs of positive selection as indexed by the linkage disequilibrium decay (LDD) test (discussed later). Using a similar index of selection (i.e., integrated haplotype homozygosity) but also the HapMap data, Voight, Kudaravalli, Wen, and Pritchard (2006) also found widespread signals of very recent selection. Both studies found that many of the selection events were specific to a single population, although a significant number of events were shared by more than one population. Both studies showed that genes related to the immune system or pathogen response are overrepresented, which would be expected given the ongoing fight for human survival against the changing environment and against other organisms, including microorganisms. Other overrepresented categories included genes associated with the cell cycle, DNA and protein metabolism, reproduction, and, of particular relevance to human behaviors, neuronal genes. Subsequent studies (Barreiro, Laval, Quach, Patin, & Quintana-Murci, 2008; Grossman et al., 2013; Lopez Herraez et al., 2009; Pickrell et al., 2009; Williamson et al., 2007) have further confirmed and expanded on the initial findings (for reviews, see Akey, 2009; Fu & Akey, 2013; Kelley & Swanson, 2008; Nielsen, Hellmann, Hubisz, Bustamante, & Clark, 2007; Pool, Hellmann, Jensen, & Nielsen, 2010; Sabeti et al., 2007; Scheinfeldt & Tishkoff, 2013).

Moreover, Hawks, Wang, Cochran, Harpending, and Moyzis (2007) further discovered that selection events were not evenly distributed across time, with accelerating pace following the major human out-of-Africa exodus starting approximately 50,000 years ago (Figure 21.2). More than half of the observed

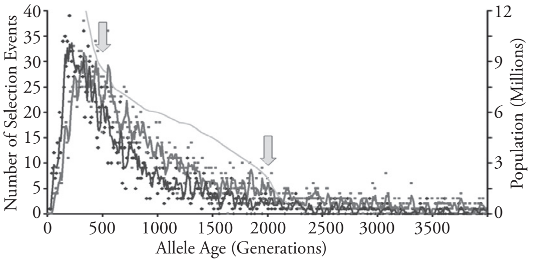

**Figure 21.2** Number of recent selection events for European ancestry populations (blue) and African ancestry populations (red). The yellow curve indicates world population size. The two arrows indicate the time of the invention of agriculture (500 generations ago) and the beginning of the Upper Paleolithic period (2000 generations ago)—the beginning of the out-of-Africa human migrations.

Source: Data from Hawks et al. (2007).

selection events dated to less than 10,000 years ago. Fu et al. (2013) showed that nearly three-fourths of all human protein-coding single nucleotide variants arose in the past 5000–10,000 years. Cochran and Harpending (2009) noted the significance of this time frame and have used the term "10,000 year explosion" to describe this burst in human population size and new mutations. Indeed, this discovery should be of great interest to cultural psychologists because this explosion took place very recently (in a historical sense) and when cultural factors came into play (from lifestyle changes such as the advent of farming to the establishment of concentrated population sites such as villages and to the invention of significant cultural artifacts such as writing systems and arts). These factors may have (1) species-wide trends, such as increasing social complexity; (2) common trends across independent groups, such as independent invention of farming in different areas of the world; or (3) group-specific cultural artifacts, such as particular writing systems, family/inheritance patterns, and so on.

Given these new data, it is now plausible to ask the following question: Which eco-cultural differences across populations of humans have posed differential selection pressures? Matching such patterns based on archaeological and anthropological data with the molecular evolution data can help paint a picture of gene–culture coevolution. The time has arrived for researchers to empirically and systematically test classic theories about gene–culture coevolution such as those proposed by Cavalli-Sforza and Feldman (1981), Lumsden and Wilson (1981), Boyd and Richerson (1985; see also Richerson & Boyd, 2005), and, recently, Laland and Obrien (2010), who proposed the niche construction theory. These theories focused mainly on mathematical models of potential gene–culture coevolution, but now they can be rigorously tested with specific genetic and behavioral data. Of course, this is just the beginning because there are many cultural dimensions and artifacts and many selected genes, but there are still very limited populations with whole-genome data.

Encouraged by the accumulating and convincing evidence that human evolution is ongoing and that many genetic changes are not neutral or even nearly neutral, researchers have examined more closely specific genes that have experienced recent selection and possibly group-specific selection. For example, researchers have examined starch in the diet and the recent evolution of the human amylase gene (Perry et al., 2007); group-specific genes related to drug absorption, distribution, metabolism, and excretion (ADME)—*CYP2C9, CYP2D6*, and *NAT2* (Li, Zhang, Zhou, Stoneking, & Tang, 2011); and group differences in the *OPRM1* gene and pain sensitivity (Hastie et al., 2012). Given that recent human history is a cultural history, it is imperative to examine how cultural factors might have guided recent human evolution. It is time to turn a disbelief into the default position that culture has shaped the human genome. The question is no longer whether culture has anything to do with genes but, rather, "how culture has shaped the human genome" (Laland et al., 2010; Richerson & Boyd, 2005; Richerson, Boyd, & Henrich, 2010).

In order to systematically yet practically address the question of culture's impact on recent human evolution, we need to focus on genes that are of most relevance to human behaviors studied by psychologists—that is, neurotransmitter genes. Neurotransmitter genes are well characterized and have been extensively studied by psychologists as candidate genes for various behaviors (e.g., *DRD2, DRD4, DAT, COMT, MAOA, 5-HTTPLR*, and *HTR1A).* Furthermore, a complete set of all neurotransmitter genes is now known from the Human Genome Project (International Human Genome Sequencing Consortium, 2004). However, with a few exceptions, such as*DRD4* (Chen, Burton, Greenberger, & Dmitrieva, 1999; Ding et al., 2002; Eisenberg, Campbell, Gray, & Sorenson, 2008; Matthews & Butler, 2011; Wang et al., 2006, *5-HTTPLR* (Chiao & Blizinsky, 2010; Way & Lieberman, 2010), and *MAOA* (Way & Lieberman, 2010), there has been little discussion on what cultural factors may be related to, or interact with, the neurotransmitter genes. Previous studies on whole-genome scans for evidence of recent selection and specific information about the evolutionary history of these genes have been beyond the reach of most psychologists. Therefore, a systematic examination and presentation of neurotransmitter genes should be of interest to psychologists (e.g., Which genes show evidence of selection, on which sites? Which allele is ancestral and which is selected in each population? and How recent did the selection event occur?). In the remainder of the chapter, we provide specific information about 131 well-characterized neurotransmitter genes, show evidence of universal and group-specific selection, present data on behavioral correlates, and discuss how this should lay the foundation for future research on cultural genomics.

## Recent Evolution of Neurotransmitter Genes

### Data Sources

To examine the recent evolution of human neurotransmitter genes, we relied on three sources of data. Our initial analysis utilized the International HapMap Project (International HapMap Consortium, 2007), which is now folded into the 1000 Genomes Project (see The 1000 Genomes Project Consortium, 2010).We focused our analyses on 270 individuals of the following groups: YRI (Yoruba, Africa), CEU (Europeans in the United States), and East Asians combining CHB (Han Chinese, Beijing) and JPT (Japanese, Tokyo). For details about these samples, see the HapMap website at http://hapmap.ncbi.nlm.nih.gov. Second, an outlier population of 38 individuals from the Riverine area of western New South Wales was analyzed (for a detailed description of the sample, see McEvoy et al., 2010). Aboriginal Australians, except for recent European admixture, have been reproductively and culturally isolated from the rest of the world for more than 40,000 years. The two previously mentioned genetic data sets have no or little relevant behavioral data collected, and they were used to examine molecular evolution. The third database—the Beijing Genes–Brain–Behavior Project—has extensive behavioral data collected with individual genotype information. Furthermore, the Beijing Project has an approximately 5- to 10-fold greater number of individuals of a particular geographic origin than the HapMap and Australian data sets, which is ideal for confirming recent selection.

Participants of the Beijing Project were 480 healthy Chinese college students (average age, 19.9 years; standard deviation (SD), 0.9; 208 males and 272 females) from Beijing Normal University. All were Han Chinese and in good health (i.e., no history of neurological and psychiatric disorders based on self-reports). DNA was extracted from blood samples. Genotyping at the neurotransmitter gene loci was conducted using standard Illumina Golden Gate Genotyping protocols (see Illumina Golden Gate Assay Protocol for details at www.southgene.com; Shanghai South Gene Technology, Shanghai, China). Whole-genome genotyping was conducted using Affymetrix 6.0 chips for 342 of the subjects, and data on all neurotransmitter gene regions were identified. In this study, extensive behavioral data (as well as brain structural and resting-state functional data, not discussed here) were collected with a battery of behavior measures covering 12 major aspects of human behaviors: perception, memory, executive function, intelligence, emotion, personality, social relationships, coping style, problem behavior, mathematical abilities, language abilities, and others (e.g., simple reaction times and Iowa Gambling Task). In general, each construct was measured with several cognitive tasks or psychological inventories, with a total of 49 tasks. The specific instruments were selected because they have been widely used in previous research and proven to have good psychometric properties. A detailed list of the measures (domain, tool name, a brief description, measurement index, number of subjects who completed the test, and references) is provided in the online supplementary materials in Chen, Chen, Moyzis, et al. (2013, Table S2).

In this initial study, we focused on 131 well-characterized genes related to the function of neurotransmitters (dopamine, serotonin, GABA, glutamate, norepinephrine, and acetylcholine). Genes related to dopamine, serotonin, glutamate, and GABA are expressed in the human brain and serve as good candidates for associations with behaviors of interest. Dopamine plays important roles in motor control, motivation, arousal, reward, and cognition, whereas serotonin regulates mood, appetite, sleep, and cognitive functions including memory and learning. GABA is the major inhibitory neurotransmitter in the central nervous system (CNS), whereas glutamate is the major excitatory neurotransmitter. Genes related to norepinephrine and acetylcholine have primary roles as hormones and at the neuromuscular junctions, respectively; however, they are also expressed in the brain and have been found to play a role in cognition (e.g., Demeter & Sarter, 2013; Doya, 2008).

### Signals of Selection

All functional genes, by definition, are subject to natural selection. Many new mutations are detrimental and hence will be eliminated. Positive selection, on the other hand, leaves clear signs in the DNA. There are several ways to find such signals of natural selection. Depending on the time depth of evolution, some signals are easier to identify than others. With greater time depth such as cross-species comparisons, researchers have counted the proportion of mutations that involve functional changes (non-synonymous mutations) versus synonymous changes (mutations that led to the same amino acid), called the $K_a/K_s$ ratio (Kreitman, 2000). Such changes are typically too rare to be a reliable index of recent evolution. Another is the fixation index

($F_{st}$), which has been used to characterize population differences (Holsinger & Weir, 2009). To study recent human evolution (<100,000 years), the most commonly used method is to assess the extent of linkage disequilibrium (or length of shared haplotypes) (e.g., Ding et al., 2002; Sabeti et al., 2002, 2007; Stephan, Song, & Langley, 2006; Voight et al., 2006; Wang et al., 2004, 2006).

Linkage disequilibrium (LD) occurs because DNA is organized like a string (or rather yoked double strand). When a new mutation arises in an individual (*DRD4* 7R as an example in Figure 21.3; Ding et al., 2002; Wang et al., 2004), it is "locked in" with all adjacent polymorphisms on that particular chromosome. If the mutation increases the individual's evolutionary success (survival and more offspring), it will increase in frequency in subsequent generations. Due to the stringlike organization, the mutation "drags" along the entire stretch of DNA around it (from the original individual) and passes the whole stretch to subsequent generations, creating LD among the neighboring nucleotides. This somewhat cumbersome term is in contrast to "linkage equilibrium," the condition in which adjacent polymorphisms are random with respect to each other—the expectation if adaptive selection is not present. A single allele at high frequency and extensive LD (in comparison to the alternative allele) is a powerful indicator of recent adaptive selection. Over time, recombination and new mutations will gradually break up the LD. Because recombination and new mutations occur randomly, the number of mutations and the chance of recombination increase with the distance between the mutation and a given nucleotide. Consequently, the breakup of LD shows a characteristic U-shaped LD Decay (LDD) curve (Figure 21.4). This LDD shape shows the signal of positive selection, and it helps distinguish selection from other causes of extended LD such as admixture (Wang et al., 2006). Moreover, in combination with the recombination rates and allele frequencies of a given nucleotide, one can also calculate the coalescence age of the selected allele (i.e., an estimate of how long ago the different individuals in the sample can trace back to a common ancestor with that mutation) (see Figure 21.4 for the formula and the figure caption for explanations of the terms; for details, see the following: Ding et al., 2002; Hawks et al., 2007; Wang et al., 2004, 2006).

### *Results*

Table 21.1 shows which of the 131 neurotransmitter genes showed evidence of recent selection, using the LDD test. Evidence for recent selection in at least one of the geographic groups examined was found for 48 genes, with at least 55 selection sites. The numbers do not match because (1) some of the genes are located too close to each other on the chromosomes to distinguish whether they are involved in the same or separate selection sites; and (2) some genes are very large and have evidence for more than one selection site, often in different populations. In terms of the variations across the gene systems, serotonin-related genes appeared to have experienced the largest amount of selection, with a majority of their genes showing evidence of recent selection. The dopamine, GABA, and glutamate systems also showed a significant number of selected genes. Few of the genes related to the non-CNS (i.e., acetylcholine and norepinephrine) showed evidence of selection. Within each system, most of the selected genes were receptor genes, perhaps because they are the most abundant type of neurotransmitter genes and directly regulate the amount of post-synaptic neurotransmitter, thus controlling the

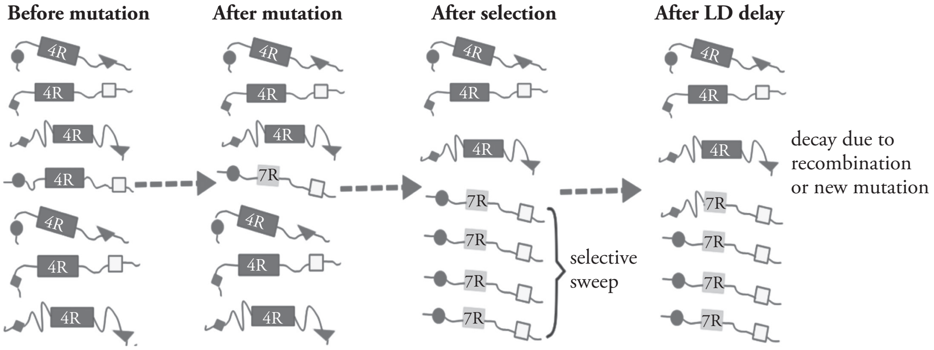

**Figure 21.3** A schematic display of the process from mutation to linkage disequilibrium (LD) as a result of selection and to LD decay.

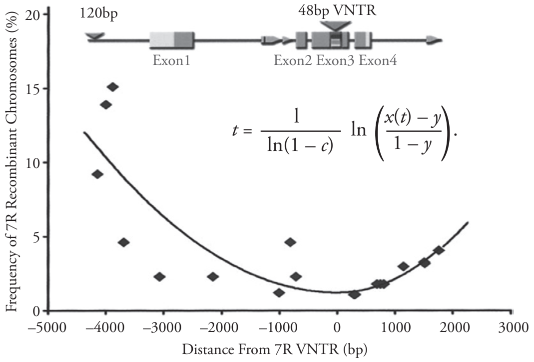

**Figure 21.4** Linkage disequilibrium decay curve: the example of *DRD4* VNTR. In the formula for allele age calculation, $t$ is allele age (in generations), $c$ is recombination rate * distance, $x(t)$ is frequency in generation $t$, and $y$ is baseline frequency. For more details, see Ding et al. (2002) and Wang et al. (2004).
Source: Adapted from Wang et al. (2004).

biochemical processes between neurons. However, genes for other subsystems (i.e., transporter genes such as *SLC6A4* and *SLC6A12*; degradation-related genes such as *MAOA* and *MAOB*; synthesis-related genes such as *DDC, TPH1*, and *TPH2*; and modulatory genes such as *NTS* and *NLN*) also showed evidence for recent selection.

The LDD data also showed that the coalescence age of the selected neurotransmitter genes was very young, with a mean age of 280 generations (SD, 227 generations) or approximately 5000–7000 years. The average allele age was significantly or marginally older for YRI (mean, 376; SD, 259) than for the other groups (265 [230] for CEU, $p = 0.045$; 281 [210] for CHB/JPT, $p = 0.067$; and 271 [226] for the Beijing sample, $p = 0.067$), which was consistent with previous literature on genetic diversity and population histories related to the out-of-Africa hypothesis. Many selected alleles in the African YRI population show a significantly older coalescence because non-African populations experienced significant bottlenecks during the out-of-Africa migration (Hawks et al., 2007; Wang et al., 2006). Allele age was not calculated for the Australian data because of its small sample size.

Next, we examined group similarities and differences. As Table 21.2 shows, of the 55 selected sites, 50 showed evidence of selection for CEU, 50 for CHB/JPT and the Beijing sample, 29 for YRI, and 20 for AUS ($\chi 2$ (3) = 19.6, $p = 0.0006$). Eleven of the 55 selected sites were common across the groups. Large differences were seen between CEU/Asians and AUS: 31 of the 50 sites showing recent selection in CEU did not show such evidence for AUS, whereas 30 of the 50 sites showing recent selection in Asians did not show such evidence for AUS. We hasten to add that this evidence of divergent selection only means that the selection of these particular genes varied by group. Similar phenotypes could have been selected via other genes, namely convergent selection.

Figures 21.5 and 21.6 show examples of the group similarities (Figure 21.5A) and three types of differences in natural selection: different genes of the same function groups (Figure 21.5B), different allele/haplotype of the same section of the gene (Figure 21.5C), and different sections of the same gene (Figure 21.6).

To investigate what behaviors were actually linked to the newly selected gene variants, we relied on the extensive behavioral measures from the Beijing Project and the detailed SNP data from both the Illumina and Affymetrix analyses. Of the 50 sites that showed strong evidence of recent selection in this sample, one to three SNPs at or very near the center of each selection site (in order to have high enough minor allele frequency (MAF) for data analysis and to have a sufficient coverage for some of the large selection sites) were selected to help identify potential behavioral correlates of the selected gene variants. Thirty-one of these SNPs showed significant associations with one or more behavioral indices at the level of $p < 0.01$. In terms of the genetic systems, all neurotransmitter systems had sites with significant behavioral correlates (4 for the DA system, 8 for the 5-HT system, 12 for the glutamate system, 6 for the GABA system, and 1 for others). In the glutamate system, representative SNPs in a large selection site, such as *GRIA2* and *GRIA4*, seemed to have different significant behavioral correlates. Table 21.3 summarizes the results by the types of behavioral correlates.

A closer look at the correlates revealed the following patterns. In terms of school-related behaviors, most of the effects appeared to be in the direction favoring the new alleles. Specifically, three different selection sites (in the genes of *MAOB, GRIA4*, and *GABRB2*) contributed to better number processing as indexed by subjects' lower reaction time (RT) to four different tests. *MAOB* encodes for an enzyme that metabolizes amine neurotransmitters such as dopamine. There is a long line of animal and human research linking *MAOB* (as well as closely related *MAOA*) to personality but also cognitive functions (for the most recent example, see Singh et al., 2013). *GRIA4* is a glutamate receptor gene

**Table 21.1 Neurotransmitter Genes With or Without Strong Evidence for Recent Selection**

| Neurotransmitter System | Evidence for Recent Selection | No Evidence for Recent Selection |
|---|---|---|
| Dopamine-related | *DRD4, DRD5, DDC, MAOA(2), MAOB, NTS*(2), *NLN*(2) (7 genes/10 sites) | *DRD1, DRD2, DRD3, SLC6A3, TH, DBH, COMT, NTSR1, NTSR2* (9 genes/sites) |
| Serotonin | *HTR1A, HTR1B, HTR1D, HTR1E, HTR1F, HTR2B, HTR2C, HTR5B, HTR7, SLC6A4, TPH1, TPH2* (12 genes/sites) | *HTR2A, HTR3A/HTR3B, HTR3C/HTR3D/HTR3E, HTR4, HTR5A, HTR6* (9 genes, 6 sites) |
| Glutamate | *GRIA1, GRIA2, GRIA3, GRIA4(2), GRIK1, GRIK2, GRIN2A(3), GRIN2B, GRIN3A, GRID1, GRID2(2), GRM1, GRM3, GRM5*(2), *GRM8* (15 genes/20 sites) | *GRIK3, GRIK4, GRIK5, GRINA, GRIN1, GRIN2C, GRIN2D,GRIN3B, GRINL1A, GRM2, GRM4, GRM6, GRM7, SLC1A1, SLC1A2, SLC1A3, ALC1A4, SLC1A6, SLC1A7* (19 genes/sites) |
| GABA | *GABRA1/GABRG2, GABRA2, GABRA3/GABRQ(2), GABRA4/GABRB1,GABRA6, GABRB2*(2), *GABRG1, SLC6A12/SLC6A13* (12 genes, 10 sites) | *GABBR1, GABBR2, GABRA5/GABRB3/GABRG3, GABRP, GABRE, GABRD, GABRR3, GABRR1/GABRR2, SLC6A1/SLC6A11, SLC32A1* (14 genes, 10 sites) |
| Non-CNS | *ADRA2B, CHRM2*(2) (2 genes, 3 sites) | *ADRA1A/SLC18A3, ADRA1B, ADRA1D, ADRA2A, ADRA2C, ADRB1, ADRB2, ADRB3, SLC6A2, PNMT, CHAT, CHRM1, CHRM3, CHRM4, CHRM5, CHRNA2, CHRNA3/CHRNA5/CHRNB4, CHRN4, CHRNA6/CHRNB3, CHRNA7, CHRNA9, CHRNA10, CHRNB2, CHRNA1, CHRNB1, CHRND/CHRNG, CHRNE* (32 genes, 27 sites) |
| Total | 48 genes, 55 sites | 83 genes, 71 sites |

Note: Some genes are located too close together on the chromosome to allow for separate examinations of LDD and hence they are grouped into "sites." They are shown in the table as those separated by dashes.

and *GABRB2* a GABA receptor gene, both of which have been found to be candidate genes for cognitive impairments associated with schizophrenia (e.g., Makino et al., 2003; Tsang et al., 2013). Although little research has been done to link these genes to normal variations in cognitive functions, our study showed that the selected gene variants of these genes seemed to contribute to better performance in four types of number processing (i.e., comparison of auditorily presented numbers, number comparison, parity judgment, and numerosity comparison). *GRIA4* was also associated with higher performance in reading (Chinese, English, and pseudo words). In addition, one Chinese character recognition task (the recognition of rarely used, low-frequency Chinese characters) was negatively associated with the selected variant of *HTR1D*, another serotonin receptor gene. Object naming was associated with two different SNPs in opposite directions (lower RT for the new allele of *GRM1*, another glutamate receptor gene, but higher RT for the new allele of *HTR1E*, a serotonin receptor gene). One possible interpretation is that these genes are interacting to optimize the phenotype by counterbalancing each other's effects. Finally, visual–auditory learning was positively associated with the new allele.

In contrast to the school-related abilities, in which the recently selected allele was mainly

**Table 21.2 Group Differences in the Number of Sites That Showed Recent Selection**[a]

| | YRI | CEU | C/J/B | AUS |
|---|---|---|---|---|
| No. of selected sites | 29 | 50 | 50 | 20 |
| Common with CEU | 27 | — | | |
| Common with C/J/B | 26 | 47 | — | |
| Common with AUS | 11 | 19 | 20 | — |

[a]Eleven genes showed selection for all four groups, including *MAOA, SLC6A4*, and six *HTR* genes.

YRI, Yaruba; CEU, Europeans; C/J/B, Chinese in Beijing from HapMap/Japanese in HapMap/Beijing from the Genes–Brain–Behavior Project; AUS, Australian aborigines.

associated with positive outcomes, general intelligence and memory appeared to have an opposite pattern. General intelligence (Wechsler Adult Intelligence Scale performance) as well as closely related discriminate RTs and memory (as measured by Wechsler memory test and false memory tests) were negatively associated with the selected gene variants (i.e., the new allele was associated with lower performance IQ, longer discriminate RT, poorer memory, and more false memory). The genes involved were *HTR5B* (a serotonin receptor gene), *TPH1* (a serotonin synthesis gene), and five glutamate receptor genes (*GRM1, GRIA1, GRIA2, GRIA3*, and *GRIA4*). Whereas little research has

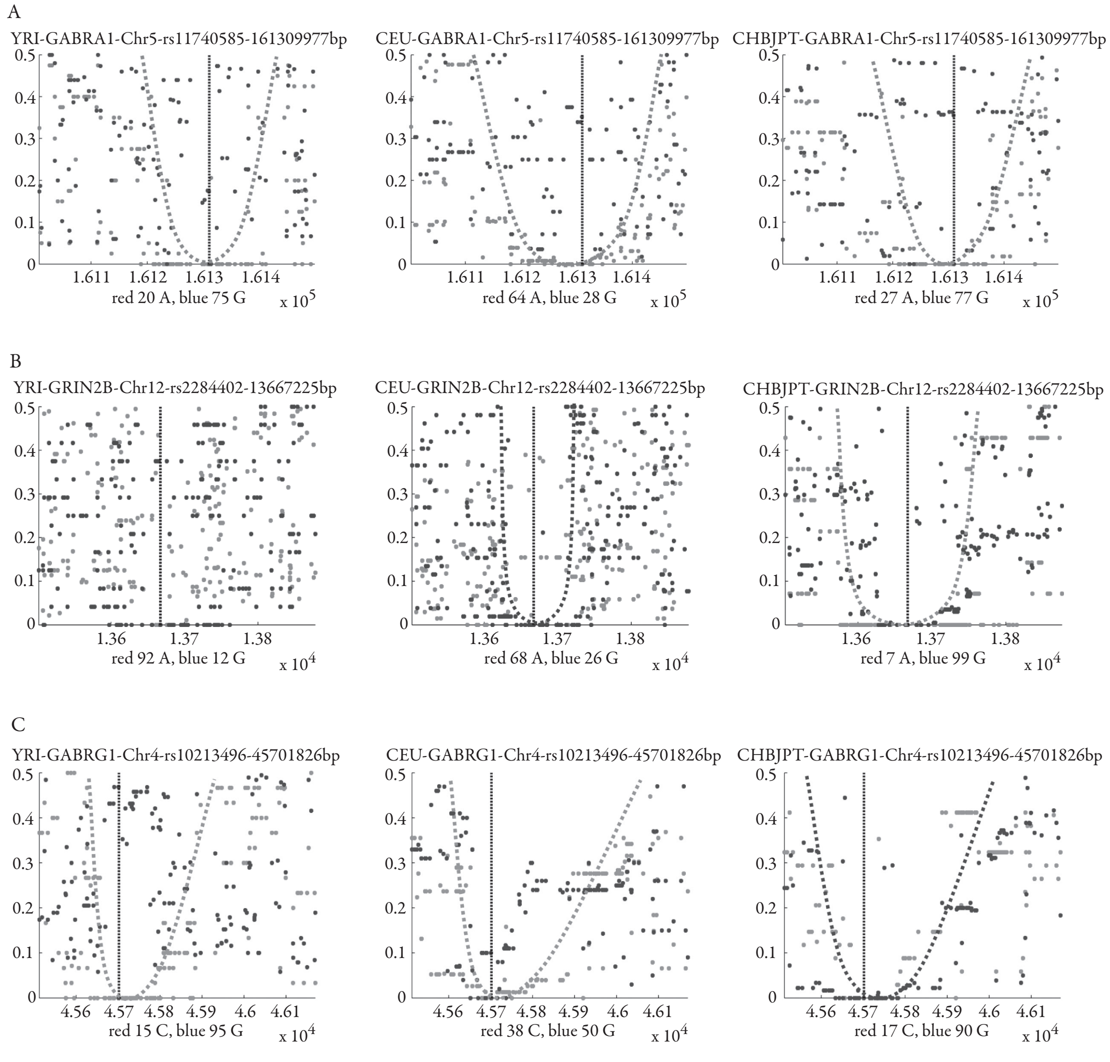

**Figure 21.5** Sample group similarities and differences in selection. Only HapMap data are shown here to allow the use of the same SNPs and to save space. (A) Same selection: A allele showed evidence of selection for all three groups. (B) Different selection: No evidence of selection for YRI, G allele was selected in CEU, but A allele was selected in East Asians. (C) Different selection: C was selected in YRI and CEU, but G was selected in East Asians.

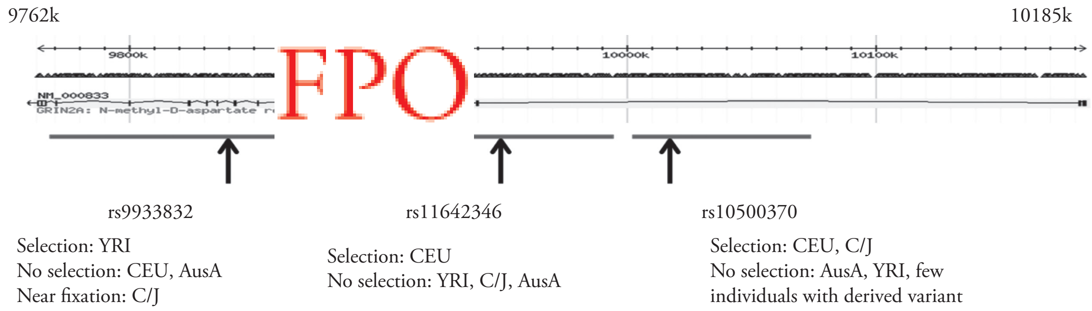

**Figure 21.6** Different selection: Same gene, but different loci. The above example is *GRIN2A,* a glutamate receptor gene. This is a large gene, with greater than 400 kbp, hundreds of SNPs, and 33 LD blocks (based on inferred haplotypes in Haploview). We identified 3 LD blocks showing strong and differential selection.

shown *HTR5B*'s implications for cognitive abilities, *TPH1* has been linked to creativity (Reuter, Roth, Holve, & Hennig, 2006), and the glutamate receptor genes have been studied for their roles in cognitive functions (for review, see Traynelis et al., 2010). Similar to the intelligence results, the selected alleles of *DRD5* (a dopamine receptor gene related to regulation of attention, memory, and learning) and *GRM8* (a glutamate receptor gene that is also involved in memory and learning) were associated with poorer facial emotion recognition.

In contrast to general intelligence and facial emotion recognition, executive and related functions such as working memory appeared to have both positive and negative associations. Each of the executive function measures was associated with two or more SNPs in opposite directions (for details, see Table 21.3). Similarly, music pitch discrimination was associated with two SNPs in opposite directions. Finally, the selected gene variant of *HTR7* (a serotonin receptor gene) was associated with better reasoning (as measured with Raven's Advanced Progressive Matrices), and the selected gene variants of *GABRA6* (a GABA receptor gene) and *GRIA2* were associated with better face memory. One can speculate that reasoning ability is closely linked to modern schooling, and face memory may be of particular importance with the increasing circle of people with whom modern humans have to interact.

In terms of personality traits, selected gene variants were linked to lower self-directedness (two genes, *HTR1E* and *CHRM2*, the latter being a muscarinic cholinergic receptor gene) but higher harm avoidance (*HTR1E*) and self-transcendence (*GRIA2*), and lower persistence in one case (*NLN*, a neurolysin gene involved in post-synaptic modulation of dopamine) and higher persistence in another (*GRID2*, another glutamate receptor gene). Like persistence, the behavioral approach system (BAS) was negatively associated with two selected variants (*NLN* and *HTR2B*) but positively associated with two other selected variants in the same gene (*GABRQ*, another GABA receptor gene). Other personality-related behavioral patterns that were linked to selected gene variants included lower intrinsic motivation (*NLN*), lower depression (*GABRQ*) but higher anxiety (*HTR1B*), more coping (active coping [*GRIK2*, a glutamate receptor gene] and negative coping [*SLC6A4*, a serotonin transporter gene]), lower self-awareness (*GRIK2*), higher emotion regulation (*GRIA3*), and better behavioral inhibition as shown by lower stop signal RT (*GRIA4*). In summary, recent selection seems to have both positive and negative genetic correlates of BAS and persistence, perhaps to optimize the phenotypes. The selection also appeared to favor traits such as harm avoidance, anxiety, behavioral inhibition, emotion regulation, stress coping, and low self-directedness, self-awareness, and intrinsic motivation. These traits appear to point toward "trying to fit in and cope"—that is, a certain degree of fear of and anxiety about the others, and good skills at self-regulation (better emotion regulation, greater behavioral inhibition, more ways of stress coping, less self-awareness, and less self-driven such as self-directedness and intrinsic motivation). In that sense, the lower depression (which reflects better coping and emotion regulation) for a selected gene variant also fit the interpretation.

## *Conclusions and Discussion*

The availability of genomic data from different cultural groups has made it possible for cultural

**Table 21.3 Behavioral Correlates of the Selected Gene Variants**[a]

| **Behavior** | **Associated Gene Variant** | | | |
|---|---|---|---|---|
| | **Gene** | **SNP (rs No. and Location)** | **Selected Allele** | **Behavioral Level for the Selected Allele Compared to the Ancestral Allele ($p < .01$)** |
| **School-related behaviors** | | | | |
| Comparison of auditorily presented numbers (RT) | *MAOB* | rs5905512 | T | Lower |
| Number comparison (RT) | *GRIA4* | rs596100 | G | Lower |
| Parity judgment task (RT) | *GRIA4* | rs596100 | G | Lower |
| Numerosity comparison (RT) | *GABRB2* | rs4921367 (downstream) | T | Lower |
| English word reading (#) | *GRIA4* | rs596100 | G | Higher |
| Pseudo-word reading (#) | *GRIA4* | rs596100 | G | Higher |
| Pseudo-word reading (#) | *GABRG1* | rs10030781 (downstream) | C/T | Higher for T allele |
| Chinese reading (#) | *GRIA4* | rs596100 | G | Higher |
| Chinese character recognition (#) | *HTR1D* | rs2776822 (downstream) | G | Lower |
| Fast naming objects (RT) | *GRM1* | rs6930181 (upstream) | T | Lower |
| Fast naming objects (RT) | *HTR1E* | rs1935596 (downstream) | G | Higher |
| Visual–auditory learning (#) | *GRIA2* | rs17035909 | T | Higher |
| **Cognitive functions** | | | | |
| WAIS performance IQ | *HTR5B* | rs41470450 (downstream) | G | Lower |
| WAIS performance IQ | *GRIA2* | rs11100110 (downstream) | G | Lower |
| WAIS performance IQ | *GRIA4* | rs7116118 (1-upsteam) | G | Lower |
| Response time (discriminate RT) | *GRIA4* | rs7116118 (1-upsteam) | G | Higher |
| Response time (discriminate RT) | *GRIA1* | rs2926289 | T | Higher |
| Wechsler Memory Scale (# recalled) | *GRIA3* | rs5911504 (upstream) | C | Lower |
| Robust false memory | *TPH1* | rs1800532 | T | Higher |
| Overall false memory | *GRM1* | rs6930181 (upstream) | T | Higher |
| Cambridge Face Memory Test (#) | *GRIA2* | rs17035909 | T | Higher |
| Cambridge Face Memory Test (#) | *GABRA6* | rs1444740 | T | Higher |
| Facial emotion recognition (#) | *DRD5* | rs12512447 (upstream) | A | Lower |

(*continued*)

**Table 21.3 Continued**

| **Behavior** | **Associated Gene Variant** | | | |
|---|---|---|---|---|
| | **Gene** | **SNP (rs No. and Location)** | **Selected Allele** | **Behavioral Level for the Selected Allele Compared to the Ancestral Allele ($p < .01$)** |
| Facial emotion recognition (#) | *GRM8* | rs2299498 | C | Lower |
| ANT (conflict effect size) | *HTR1B* | rs16889501 (upstream) | C | Higher |
| ANT (conflict effect size) | *HTR7* | rs6583736 | C | Higher |
| ANT (conflict effect size) | *GRIA3* | rs5911504 (upstream) | C | Lower |
| WCST (preserved errors) | *NLN* | rs27139 (upstream) | C | Higher |
| WCST (preserved errors) | *GRIA4* | rs10791773 | C | Lower |
| Reasoning (RAPM) | *HTR7* | rs6583736 | C | Higher |
| Music pitch discrimination (#) | *GRIA4* | rs7116118 (1-upsteam) | G | Lower |
| Music pitch discrimination (#) | *DDC* | rs11575320 | A | Higher |
| **Personality-related, etc.** | | | | |
| TCI, Self-directedness | *HTR1E* | rs1935596 (downstream) | G | Lower |
| TCI, Self-directedness | *CHRM2* | rs4518582 (upstream 2) | G | Lower |
| TCI, Harm avoidance | *HTR1E* | rs1935596 (downstream) | G | Higher |
| TCI, Persistence | *NLN* | rs27139 (upstream) | C | Lower |
| TCI, Persistence | *GRID2* | rs10021088 | T | Higher |
| TCI, Self-transcendence | *GRIA2* | rs11100102 (downstream) | G | Higher |
| BAS | *NLN* | rs27139 (upstream) | C | Lower |
| BAS | *HTR2B* | rs2303357 | C | Lower |
| BAS | *GABRQ* | rs5924753 | G | Higher |
| BAS | *GABRQ* | rs6627611 | A | Higher |
| WPI-IM | *NLN* | rs27139 (upstream) | C | Lower |
| Beck Depression Inventory | *GABRQ* | rs6627611 | A | Lower |
| Beck Anxiety Inventory | *HTR1B* | rs16889501 (upstream) | C | Higher |
| Negative coping | *SLC6A4* | rs4598962 (downstream) | G | Higher |
| Active coping | *GRIK2* | rs9399712 (downstream) | T | Higher |
| Internal self-awareness (ISA) | *GRIK2* | rs9399712 (downstream) | T | Lower |
| Emotion regulation | *GRIA3* | rs5911504 (upstream) | C | Higher |
| Stop signal (SSRT) | *GRIA4* | rs17383466 (upstream) | C | Lower |

[a]See Chen, Chen, Moyzis, et al. (2013) supplementary Table S2 for details of behavioral measurements. Allele labeling was consistent with the HapMap system. Unless otherwise indicated, centers of selection were on the gene labeled. Gene–behavior associations were analyzed using Plink (additive model).

ANT, Attention Network Test; BAS, behavioral approach system scale; RAPM, Raven's Advanced Progressive Matrices; RT, reaction time; SSRT, stop signal reaction time; TCI, Temperament and Character Inventory; WAIS, Wechsler Adult Intelligence Scale; WCST, Wisconsin Card Sorting Task; WPI-IM, Work Preference Inventory–Intrinsic Motivation; #, number of correct response.

psychologists to search for cross-cultural similarities and diversities in the human genome and to examine what cultural factors might have been involved in both species-wide and group-specific recent evolution. Results of this study provided a detailed picture of evidence for recent evolution in neurotransmitter genes. A large number of neurotransmitter genes showed evidence of recent selection. This was especially true for the four neurotransmitter systems that are most important for the CNS. Interestingly, we found that serotonin genes were especially likely to have experienced selection. Serotonin is linked to functions such as intestinal contraction and appetite (because 90% of this neurotransmitter is in the intestines), but it is also associated with functions such as mood, sleep, memory, and learning (with 10% serotonin in the brain). GABA is mainly an inhibitory neurotransmitter. These genes appear to be important in adapting to increasing complex societies or, as other researchers have speculated, humans' tendency to "self-domesticate" ourselves, a point to which we later return (Albert et al., 2012).

Both similarities and differences were found among the groups of subjects examined. In terms of diversities, the sources can be different genes, different sections of the same gene, and different variants. The finding of fewer selection events for YRI and AUS supports the idea that many of the selection events are recent. In the case of AUS, this population has been reproductively isolated for more than 40,000 years. Moreover, AUS did not develop agriculture, a factor believed to be important for many recent selection events, as mentioned previously (Hawks et al., 2007; Wang et al., 2006).

We also found that the selected gene variants were associated with better school-related skills but poorer performance in a number of social, emotional, and cognitive tasks. On the surface, the latter finding was surprising, but it is consistent with the notion of human self-domestication. Domesticated animals have consistently shown various features of the domestication syndrome, such as smaller teeth (especially canines), floppy ears, curly tails, smaller brains, and diminished fear-arousal response. As Leach (2003) speculated, this phenomenon could be of relevance to human evolution because humans are regarded as "self-domesticated" higher primates. Indeed, as one example of evidence consistent with human self-domestication, skull measurements have shown that the human brain appears to have been shrinking during the past few thousand years (Hawks, 2011). According to John Hawks, archaeological data show that brains have shrunk approximately 150 $cm^3$ from a mean of approximately 1350 $cm^3$ (i.e., slightly more than 10%) in the past 10,000 years, and this decline was consistent in different continents. Compared to hunter–gatherer preliterate lifestyles, humans today rely more on (1) other humans for many tasks (while each individual is more specialized) and (2) external tools to store and process information. Counterintuitive as it may seem, we might not need our brains as much (Hawks, 2011). Similarly, until very recently, humans actually experienced a decline in general health. Research has shown that pre-agriculture populations were taller and healthier (including healthier and longer teeth) than those after the invention of agriculture (Larsen, 1995; Mummert, Esche, Robinson, & Armelagos, 2011). In summary, humans have had to adapt to the physical and cultural environments they have created for themselves, and these environments in turn have exerted selection pressure (not necessarily all for the better) on the human body and brain.

Several limitations of the study need to be mentioned. First, several factors might have affected the estimates of the number of recently selected genes. On the one hand, our number may have been an underestimate for several reasons. First, despite the 5- to 10-fold larger sample size of the Beijing Project, the sample size was still limited when used to analyze LDD from homozygotes (which were needed to avoid the noise from inferred haplotypes; Garrick, Sunnucks, & Dyer, 2010; Mensah et al., 2007). Selected alleles with frequencies less than 0.10 would be difficult to detect in this sample with the current LDD method. Second, the existing whole-genome data still have incomplete and biased coverage of the genome (Drago, De Ronchi, & Serretti, 2007; Jiang et al., 2003; Ross et al., 2013; Saccone et al., 2009). Third, there are many other genetic polymorphisms, such as copy number variations (CNVs), that were not analyzed. On the other hand, we might also have overestimated selection events due to genetic admixture in the data (which artificially increased extended haplotype) and the inclusion of related individuals in the same database (which is somewhat of an issue for both CEU and Australian data in the current study). Extensive simulations of these potential problems, however, have suggested that the LDD test is not sensitive to admixture, inversions, and related individual inclusion (Wang et al., 2006).

Second, like most gene–behavior association studies, this study did not directly examine the biochemical functions of the SNPs, nor is there much existing information about them. Note that many of the SNPs are in the noncoding regions, so their functions most likely include regulation of mRNA expression and splicing (The ENCODE Project Consortium, 2012; Zhang et al., 2007). On the other hand, our results were based on all major neurotransmitter genes and a large battery of behaviors, which should overcome typical issues involving research with a single SNP and a single behavior. It is hoped that our results will spur research into the biochemical functions of the recently selected gene variants, as well as other physiological/phenotypic associations (Grady et al., 2013).

Third, our behavioral data derived from only one cultural group. Therefore, the direction of selection effect (especially those consistent with the human self-domestication hypothesis) may have been due to the particular human cultural history of the agrarian Chinese society, which emphasized collectivism and Confucianism. It is plausible that some of those effects may have shown an opposite pattern in cultural contexts such as the West that emphasize individualism. Future comparative research is needed.

Despite the previously mentioned limitations, the results of this study have important implications for our understanding of the relations between culture, genes, and behaviors. The relations among them can be greatly illuminated by an understanding of the recent evolutionary history of the human genome, including species-wide and group/context-specific changes. From the divergent evolutionary perspective, susceptibility loci for physical diseases and mental illnesses (or genes for any normal adaptions) might differ by group, which might explain some of the large number of instances of nonreplications of susceptibility loci across studies of different populations. This perspective can also extend existing discussions on gene–environment interactions (e.g., the differential susceptibility hypothesis proposed by Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2007) to cross-cultural contexts, in which both genes and environments may vary due to their evolutionary history(ies). As an illustration, Caspi et al. (2003) first found that the effect of *5-HTTLPR* on depression was moderated by early life stress (for a meta-analysis, see Karg, Burmeister, Shedden, & Sen, 2011), and yet the allele frequencies of *5-HTTLPR* vary greatly across cultures and their link to mental health is likely to be moderated at the cultural level (e.g., individualism–collectivism orientation; Chiao & Blizinsky, 2010). A better understanding of how cultures and genes have been coevolving (particularly the former's impact on the latter) should lead to culture-sensitive health policies and culture-specific, genetics-informed diagnosis and treatment of diseases. This is only the beginning of this line of work. This study aimed to lay the foundation for future research in a new field of (cross-)cultural genomics.

## The Emergence of (Cross-)Cultural Genomics and Directions for Future Research

On July 17, 1990, US President George Bush signed Presidential Proclamation 6158 designating 1990–2000 as the "Decade of the Brain." The Decade of the Brain espoused two major scientific advances that changed research on human behavior forever. The Human Genome Project was started in October 1990, and the initial draft of the human genome was announced in April 2000 (complete draft in June 2004; International Human Genome Sequencing Consortium, 2004). Also in 1990, Seiji Ogawa discovered the blood oxygen level-dependent (BOLD) contrast, which launched the age of functional magnetic resonance imaging (fMRI)-based cognitive neuroscience. These two advances opened two "black boxes" for psychologists: the brain and the genome. For a century, psychologists had tried to peek into the normal brain functions with basic S–R paradigm or introspection or EEG, none of which allows for a clear view of brain activities. Psychologists, or rather the subgroup called behavior geneticists, have also tried to assess the contributions of genes to behavior through twins and adoption studies by treating the genome as a "black box." With fMRI and genomics, the two black boxes have been opened. To the researchers' surprise, the things stored in the boxes are like Braille to a sighted person—there is visible order and structure, but their meaning is not easily discernible. The thousands of fMRI studies and molecular genetic behavior studies since 1990 have barely begun to help decode the meanings of brain activities and the functions of the genes.

Despite earlier fears about biological determinism and reductionism, one of the most significant findings from neuroscience and cognitive neuroscience is neuroplasticity. Cultural psychologists and anthropologists have deemed this as the perfect mechanism for the omnibus culture to "get deep under the skin." In edited volumes and journal special issues (Ames & Fiske, 2010; Chiao, 2009; Chiao & Blizinsky, 2010), a group of psychologists (many of whom are represented in this volume) led by Joan

Chiao has forcefully argued that indeed one can see the fingerprints of culture in brain scans. In a parallel universe, anthropologists have also embarked on a journey to create a field called neuroanthropology, which aims to integrate anthropology, social theory, and the brain sciences and to place the brain at the center of discussions about human nature and culture (Downey & Lende, 2012). According to this perspective, the brain is a cultural organ because at birth the human's nervous system is very immature and thus open to "cultural sculpting."

Similar to its impact on brain function and structure, culture can also affect genes (Figure 21.7). This can occur in two ways. First, culture can affect gene expression, often through epigenetic processes such as methylation. For example, a long line of research has documented the role of culture (broadly defined as including socioeconomic status) in physiological functioning such as the hypothalamic–pituitary–adrenal axis and gene expressions (e.g., Evans, Chen, Miller, & Seeman, 2012). Similarly, psychosomatic stress can modulate human gene expression, physiological function, and, consequently, psychological functioning.

Second, culture can also act as a selection agent and alter gene frequencies. In other words, over the millennia, culture has left its fingerprints on our genomes. From this perspective, instead of building a biological constraints model of gene–culture coevolution as was done in earlier attempts, but especially that by Lumsden and Wilson (1981), we need to focus on culture-driven evolution. Biology provides the raw materials, but culture actually shapes them into a biocultural entity. Biology is like the producer of a movie or the manager of a sports team, but culture is like the director or the coach. Neither can make a successful movie or a winning team without the other, but the latter is more likely to be credited for success and blamed for failures. So should culture in the long process of evolution.

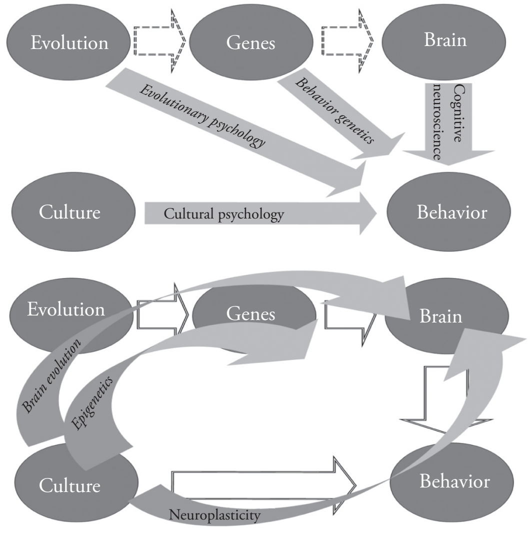

**Figure 21.7** The "encultured" brain: three routes of culture's influence on the brain.

## *Future Directions and Related Issues*

As mentioned previously, this field has barely started, so most work is yet to be done. There are many directions this work can take. First, with the general framework outlined about how culture can impact the genome, researchers can begin to conduct hypothesis-driven studies. The first step in that work is to identify cultural processes (with anthropological and archaeological evidence) that may have been responsible for convergent or differential selection. Some basic criteria for selection agents include relative stability over time, identifiable genetic/biological bases for the relevant behavior, and demonstrable advantages of the given behavior in survival and fitness in the presence of the selection agent. Candidate genes can then come from the identified genetic system, and their associations with behaviors can be studied at both group and individual levels. Major selection agents include some processes that have been discussed in the literature, such as migration and associated lifestyle (e.g., its effect on *DRD4*; Chen et al., 1999; Matthews & Butler, 2011) and collectivism (e.g., its moderation of the effect of *5-HTTLPR* (Chiao & Blizinsky, 2010) or of *OXTR* (Kim et al., 2010)). Factors to be explored may include social dominance, social complexity, and cognitive development. Sometimes, one cultural event such as the invention of agriculture may have cascading effects on many aspects of social behaviors. Given that many societies had independent development of agriculture and many did not develop it (e.g., Australian aborigines, as mentioned previously), replications from different comparisons can be used to strengthen the evidence. In Chen et al. (1999), for example, different migration routes were used to cross-validate the hypothesized association between migration and the *DRD4* gene.

Second, we illustrated the diversity in the human genome in this study, but to fully understand culture's impact on the human genome, much more genetic data are needed. The 1000 Genomes Project database will eventually contain information about the genetic variation from more than 2000 subjects from more than a dozen countries. However, individual-level behavioral and genetic data will eventually be needed to fully address how culture affects the genome. Note that unless each subject's genome is sequenced, SNP data are bound to be incomplete (especially regions that are difficult to genotype such as the region near the *DRD4* VNTR, for which there are few SNPs in the HapMap data; Saccone et al., 2009), and other variations such as CNVs are often missing.

Third, increasingly more research has indicated that epigenetic processes and/or gene–gene and gene–environment interactions may have been responsible for group differences in gene–behavior associations. For example, we recently found that the association between the *COMT* gene and working memory as well as associated brain structure varies by cultural group (Wang et al., 2013). Similarly, Kim and her group (Chapter 19, this volume) found cultural differences in *OXTR*'s effect on social support and well-being. There is also much evidence of gender-specific effects of genes on behavior (e.g., Chen, Chen, Moyzis, Dong, et al., 2011; Dmitrieva, Chen, Greenberger, Ogunseitan, & Ding, 2011; Harrison & Tunbridge, 2008; Jazin & Cahill, 2010). Of course, some of these group-specific effects may just be inconsistent results due to random factors, so more research is also needed to sort these group-specific genetic effects into random effects (Chabris et al., 2012) and true group-specific effects.

In addition to long-term cultural selection, short-term selection pressures can also shift subpopulations' genetic structure. Recently, we demonstrated that college enrollment represents not only a social stratification but also genetic stratification (Chen, Chen, Moyzis et al., 2013). We found that 24 of the 284 SNPs of neurotransmitter genes included in our study showed significant Hardy–Weinberg deviations (HWDs) in our college sample in comparison to population-based controls. These deviations were likely due to social selection because these loci were found to be associated with mathematical abilities, executive functions, motivation, and adjustment-related behaviors such as alcohol use. Generally, genotypes overrepresented in the college sample showed better performance and adjustment than underrepresented or nonbiased genotypes. Interestingly, half of the HWDs were gender-specific, as were their behavioral effects, which is consistent with a growing literature on gender-specific gene effects, as mentioned previously.

Fourth, although the human genome has been sequenced, the biochemical functions of most genes are not well understood, as mentioned previously. In order to completely understand recent human evolution involving particular genes, we need to understand their biochemical mechanisms. These mechanisms need to be understood at the individual gene variant level as well as the gene-system level because of complex gene–gene interactions. As mentioned previously, natural selection can work on the same gene variant or a different gene variant that serves the same function (e.g., dopamine level can be controlled by any of the subsystems, namely synthesis, receptor, degradation, and modulation); thus, a system-level approach or pathway analysis of gene–behavior associations is needed (for examples, see Chen, Chen, Moyzis, et al., 2013; Chen, Chen, Moyzis, Stern, et al., 2011).

## Concluding Remarks: The Encultured Genome

The strong evidence of recent human evolution and the idea that human activities and human culture have shaped recent human evolution have turned the common notion of the biological bases of human behavior on its head. The biological entity of a human is as much a product of culture as culture is a product of the collective of biological entities. Researchers have begun to push to redefine the current geological epoch as the Anthropocene (Balter, 2013) to indicate the importance of human activities in shaping the world, including humans themselves. Culture constantly shapes the brain and, over time, shapes the genome. Indeed, culture gets under the skin deeply and into the genome. With the modern neuroimaging and genomic tools and the advent of the field of cultural neuroscience, we can now study how the brain and the genome are "encultured"—how culture has put its fingerprint on the brain and the genome. This line of work should help shift from the traditional view of gene–culture coevolution, which was often reduced to some form of biological determinism (sociobiology), to a new form with culture as a driving force in the ongoing mutual construction of culture and biology. Culture may just be the most important force of recent natural selection for humans.

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# PART 7

# Linking Population Health Disparities and Cultural Neuroscience

## CHAPTER 22

# The Role of Culture in Population Mental Health: Prevalence of Mental Disorders Among Asian and Asian American Populations

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## Abstract

In recent years, studies of population mental health have increased in number, and assumed growing importance, in psychiatric epidemiology and global mental health. These studies have enabled valuable estimates of psychopathology across different countries and cultural settings, thus providing assessment of the global burden of mental illness. They have also progressively grown in size and complexity, which has resulted in the use of more reliable methodologies to assess psychopathology. Fundamental challenges in what constitutes syndromes of "mental illness" (e.g., "major depression") in terms of incorporating culture-specific features of psychopathology across cultural settings have also resulted from conducting these studies across differing cultural contexts. This has spurred further evolution in the conceptualization of and methodologies used to assess mental illness. This chapter highlights population studies in mental disorders among Asian and Asian American groups as a specific example to illustrate how culture affects the prevalence, assessment, and manifestation of psychopathology.

**Key Words:** psychiatric epidemiology, global mental health, culture, Asians, Asian Americans, mental health, prevalence, psychopathology, diagnosis

## Overview

In recent years, studies of population mental health have increased in number, and assumed growing importance, in psychiatric epidemiology and global mental health. First, these studies have enabled valuable estimates of psychopathology across different countries and cultural settings, thus providing assessment of the global burden of mental illness. These studies have also progressively grown in size and complexity, which has resulted in the use of more reliable methodologies to assess psychopathology. Fundamental challenges in what constitutes syndromes of "mental illness" (e.g., "major depression") in terms of incorporating culture-specific features of psychopathology across cultural settings has also resulted from conducting these studies across differing cultural contexts. This in turn has spurred further evolution in the conceptualization of and methodologies used to assess mental illness.

This chapter highlights population studies in mental disorders among Asian and Asian American groups as a specific example to illustrate how culture affects the prevalence, assessment, and manifestation of psychopathology. Because prior extensive reviews of mental illness within Asian and Asian American groups have emphasized non-population-based samples (Yang & Wonpat-Borja, 2006, Kalibatseva & Leong, 2011), this chapter primarily focuses on studies derived from the recently conducted National Latino and Asian American Study (NLAAS). We choose to highlight the NLAAS because it is the sole representatively sampled study of Asian Americans, and it provides a unique opportunity to address key questions regarding the nature, manifestation, and prevalence of psychopathology among Asian Americans. Furthermore, this study was the first major psychiatric epidemiology study to enable examination of distinct subgroups of Asian Americans (Chinese, Filipino, and Vietnamese, along with an "Other Asian" subgroup that includes Koreans, Cambodians, and Asian Indians) rather than collapsing Asian Americans into one homogenous group. Finally, this study, with its size and representative nature, allows the investigation of how central constructs linked with immigration, such as ethnicity, race, acculturation, and social factors, influence psychopathology.

We seek to answer these key questions by first introducing how cultural processes organize experiences of distress in ways congruent with the social context, thus shaping the manifestation of psychopathology. We briefly examine the use of somatic metaphors among Asians as an example of a culturally mediated form of distress. Next, we provide an overview of the prevalence of mental disorders in the United States by describing three major psychiatric epidemiology studies that examine the US general population and major ethnic minority groups in the United States (African Americans, Latino Americans, and Asian Americans). In the next major section, we review cultural issues of relevance to the prevalence and manifestation of psychopathology among Asian Americans. We begin by reviewing findings from a groundbreaking psychiatric epidemiology study of the prevalence of mental disorders in China to identify cultural influences on mental health that might exist within a native Asian context. We then describe how immigration processes to the United States may modify the experience of psychopathology among Asian Americans, followed by a critical analysis of differences in diagnostic methodologies used to define the presence of psychopathology and how these might impact estimates of prevalence. We then evaluate the psychopathology research on Asian Americans, highlighting mental health utilization studies and research on substance abuse, anxiety, major depressive, and schizophrenia spectrum disorders. We then describe potential mechanisms that might underlie cultural differences in mental disorders among Asian Americans, including gender effects, loss of subjective social status, acculturative stress, and discrimination. We conclude by outlining future directions for the field and possible directions that cultural neuroscience might take to inform population mental health.

## Culture and Psychopathology

### *How Cultural Processes Influence Psychopathology: Somatization Among Chinese Groups*

Culture can be conceptualized as a dynamic process that permeates both larger- (economic and political) and smaller-scale (psychological and biological) social forces. Culture can be viewed via the concept of "moral experience," whereby "what is most at stake" during everyday activities for ordinary participants in their social contexts in turn imbues events such as illness with emotional meaning for actors in local worlds (Kleinman, 2004). Cultural processes, by shaping interpretation of subjective experiences of physiology and distress, thereby influence the experience and manifestation of psychopathology. First, culture shapes how symptoms are expressed and experienced, which subsequently may affect course of illness. Second, although certain symptoms may share core features across cultures (e.g., hearing voices), how these symptoms are responded to are shaped by cultural meanings and interpretations (e.g., seen as spirit possession and brought to a religious healer). Third, identical symptom patterns may be classified as differing syndromes altogether according to changes in historical and sociopolitical trends (Lee, 2002). Accordingly, cultural meanings and everyday practices shape how distress linked with mental illness symptomatology is manifested, organized, and responded to within a particular social context.

One such cultural preference for how emotions are experienced and expressed occurs within Chinese groups via somatization, which describes a specific clinical presentation in which somatic symptoms are emphasized while psychological, emotional, or social difficulties are minimized (Kirmayer & Young, 1998). Although somatization takes place in all cultures, Chinese cultural groups may exhibit an especially high prevalence of somatization because emotional communication occurs not in words that represent emotion but instead through somatic or bodily metaphors (Cheung, 1995). This conceptualization acknowledges that affective and somatic symptoms can coexist (even if physiological expressions are currently emphasized) and that somatization reflects a culturally mediated way of tapping into local ideas about how the body conveys distress that is located within interpersonal and broader cultural models of illness.

Somatization may also be experienced as a construction of illness distress by the patient to avert the severe stigma associated with psychiatric diagnoses that may threaten "face" and social standing (Yang, Phelan, & Link, 2008; Yang et al., 2007). Despite this tendency for Chinese groups to utilize bodily metaphors to express emotional distress upon open-ended questioning (Kleinman, 1977) or unstandardized interview (Hsu & Folstein, 1997) in outpatient medical settings, general community groups (Zhang, Snowden, & Sue, 1998) or samples interviewed with structured questioning (Yen et al., 2000) indicated that Chinese groups actually endorse equivalent levels of affective distress (e.g., depressed mood) compared with Anglo groups. Thus, for Chinese Americans, it appears that somatic complaints are frequently and spontaneously endorsed when affective distress (e.g., depressive symptomatology) is present. However, although somatic complaints act as a preferred means of communicating distress, these act in parallel with affective complaints to express psychological suffering.

### *Prevalence of Mental Disorders in the US General Population and Major Ethnic Minority Groups*

Having introduced an example of how culture might shape manifestation of psychopathology, we now turn to a discussion of population mental health. To frame our discussion on psychopathology among Asian American groups, we present an overview of population mental health in the United States based on the National Institutes of Mental Health Collaborative Psychiatric Epidemiology Surveys (CPES) initiative, a national household survey of 20,013 adults age 18 years or older. The CPES included three nationally representative surveys: the National Comorbidity Survey Replication (NCS-R; sampling the general US population; Kessler et al., 2005), the National Survey of American Life (NSAL; sampling African American, Afro-Caribbean, and non-Hispanic Whites; Jackson et al., 2004), and the NLAAS (sampling Latino and Asian Americans; Alegría et al., 2004).

The sampling methodologies for these studies are described in detail elsewhere (Kessler & Ustun, 2004); a brief summary is provided here. All surveys utilized multistage clustered sampling designs (Heeringa et al., 2004), which led to nationally representative household sampling for all studies. In brief, these studies follow a core four-stage area probability design to sample (1) US metropolitan statistical areas and counties, (2) area segments, (3) housing units, and (4) respondents (Kessler & Ustun, 2004). For the NSAL, we describe findings for the African American group only, who self-identified as Black but did not report Caribbean ancestry. For the NLAAS, these core sampling strategies were augmented by high-density supplemental sampling, which was utilized to oversample census block groups with greater than 5% density of target ancestry groups (i.e., Latino or Asian ancestry). Recruitment of secondary respondents in the NLAAS was also obtained from households in which one eligible member had already been interviewed. The data were weighted to account for differential probabilities of selection, differential non-response, and differences in sociodemographic variables between the sample and 2000 Census population. Interviews were carried out in person in most instances (with telephone interviews being conducted in special circumstances) by highly trained lay interviewers utilizing computer-assisted interviewing software. Interviews of ethnic minority group members took place with trained bilingual interviewers who shared similar linguistic and cultural backgrounds with the target population.

All CPES studies utilized the World Mental Health Survey Initiative Version of the World Health Organization Composite International Diagnostic Interview (WMH-CIDI), a fully structured diagnostic interview that generates *Diagnostic and Statistical Manual of Mental Disorders*, fourth edition (DSM-IV; American Psychiatric Association, 1994) diagnoses (Kessler & Ustun, 2004). A key characteristic of the CIDI is that it is administered by trained non-clinicians who ask a set of standardized questions with fixed responses to establish diagnosis. The CIDI begins with a set of screening items that, if answered affirmatively, lead to more in-depth questions about specific symptom criteria. For example, if a respondent answers affirmatively to ever having experienced depressed mood every day or nearly every day during a 2-week period, the structured questions for major depression would subsequently be administered item-by-item. Diagnoses are then established by computerized scoring algorithms based on respondent answers. WMH-CIDI diagnoses for anxiety, mood, and substance use disorders have adequate to good reliability (impulse-control diagnoses were not validated) with blind clinical re-interviews with the Structured Clinical Interview for DSM-IV (SCID), which are currently considered the gold standard of diagnosis in population studies (Haro et al., 2006).

Lifetime and 12-month prevalence was established for mood disorders (major depressive disorder), anxiety disorders (panic disorder, agoraphobia, social phobia, generalized anxiety disorder, and post-traumatic stress disorder), substance disorders (alcohol abuse, alcohol dependence, drug abuse, and drug dependence), and any disorder (any depressive, anxiety, or substance use disorders as defined previously). Age of onset was recorded for each disorder endorsed by respondents. Whereas the NCS-R includes other anxiety disorders (specific phobia, obsessive–compulsive disorder, and separation anxiety disorder), mood disorders (dysthymia and bipolar I and II disorders), and "impulse control disorders" (intermittent explosive disorder, oppositional-defiant disorder, conduct disorder, and attention deficit hyperactivity disorder), these were not assessed in the NSAL and NLAAS studies and thus are not included in our comparisons (Table 22.1). Schizophrenia was not assessed by any of the CPES studies because lay-administered diagnostic instruments significantly overestimate schizophrenia prevalence. Demographic variables, including age, sex, race/ethnicity, years of education, employment status, and marital status, were self-reported by respondents. Supplemental measures of immigration included (1) nativity status (US-born or foreign-born), (2) age at time of US immigration, (3) years of US residency, and (4) generational status (first generation—immigrants; second generation—born in the United States to at least one immigrant parent; and third generation or later—born in the United States to US-born parents and had at least one grandparent who was immigrant-born or neither parents nor grandparents were immigrant born but respondent self-reported being from a particular ethnic group).

Sample descriptions, response rates, sampling periods, and lifetime prevalence of mental disorders in the US general population and three major ethnic minority groups (African American, Latino American, and Asian American) are summarized in Table 22.1. On first observation, the lifetime prevalence of "any disorder" appears to be higher in the US general population (46.4%) compared with the three ethnic groups (17.9–30.5%). However, the higher prevalence among the US

**Table 22.1 Comparison of Lifetime Prevalence Rates of Mental Disorders Among the General US Population and Three Major Ethnic Minority Groups**

| | **General US Population NCS-R (Kessler et al., 2005)** | **African American NSAL (Williams et al., 2007)** | **Latino American NLAAS (Algeria et al., 2008)** | **Asian American NLASS (Takeuchi et al., 2007)** |
|---|---|---|---|---|
| Any disorder (%) | 46.40 | 30.50 | 29.70 | 17.90 |
| Any anxiety disorder (%) | 28.80 | Not available | 15.70 | 9.80 |
| Any major depressive disorder (%) | 16.60 | 10.40 | 15.20 | 9.10 |
| Any substance disorder (%) | 14.60 | 11.50 | 11.20 | 4.00 |
| Any impulse control disorder | 24.80 | Not assessed | Not assessed | Not assessed |
| Sample characteristics | 9282 English-speaking household residents | 3570 African American household residents | 2554 English- and Spanish-speaking Latino household residents (Mexican, Puerto Rican, Cuban, and Other) | 2095 Asian American household residents (Chinese, Filipino, Vietnamese, and Other) |
| Response rate (%) | 70.90 | 70.70 | 75.50 | 65.60 |
| Sampling period | February 2001–April 2003 | February 2001–June 2003 | May 2002–December 2003 | May 2002–November 2003 |

general population may at least be partially attributable to the fact that the NCS-R included the lifetime assessment of "any impulse control disorder" (24.8%), which was not assessed in the NSAL or NLAAS studies. Nevertheless, when examining prevalence rates within each specific class of disorder, it appears that prevalence in the US general population remains higher than rates found within the other groups. For example, prevalence of any substance disorder is the highest in the US general population (14.6%) compared with that from the other three ethnic groups (4–11.5%). Another general pattern is that among the African American and Latino American groups, prevalence of all types of mental disorders appears to be intermediate, whereas prevalence of mental disorders within the Asian American group appears lowest. Overall, this initial comparison suggests that significant cultural variation for mental disorders exists within ethnic groups in the United States, with prevalence in the US general population appearing to be highest. As we shall examine later, although any conclusions are made much more complex when considering ethnic subgroups and immigration status, these findings provide valuable context for interpreting generational differences in psychopathology in particular. This analysis thus provides a useful launching point by which to examine how cultural influences might impact the manifestation and prevalence of psychiatric disorders among Asian Americans.

## Cultural Processes and Prevalence of Psychopathology Among Asian Americans

### *Prevalence of Psychopathology in the Asian Context: Example of China*

To further frame an analysis of the prevalence of psychopathology within Asian American groups, an informative first step is to evaluate the manifestation and prevalence of mental disorders within Asian countries. The prevalence, and types of disorders present, within such Asian contexts elucidates how mental disorders manifest within native Asian cultures and might guide understanding of how mental illnesses appear within Asian American populations. One landmark study (Phillips et al., 2009) conducted in China enables an unprecedented opportunity for initiating such an examination. Unlike other large-scale psychiatric epidemiology studies (including the US-based studies described previously) that use a structured, diagnostic interview given by lay interviewers (Kessler & Ustun, 2004), one major innovation provided by Phillips' study is the two-stage sampling design in which diagnoses were provided via a clinician-administered SCID (Yang & Link, 2009). This is the only major psychiatric epidemiology study to use a standardized, clinician-administered tool to establish diagnoses. This approach offers several advantages. First, it provides more valid detection of nonaffective psychosis (Kendler, Gallagher, Abelson, & Kessler, 1996). Due to poor reliability of lay-administered, structured diagnostic interviews in identifying nonaffective psychoses, nearly all population-based studies provide little or no data on psychotic disorders. Second, clinicians can rephrase standard SCID probes as flexible, semistructured questions in the local vernacular, thus obtaining more detailed symptom data compared with a completely structured clinical interview (Yang & Link, 2009). Third, it provides the option of diagnosing "Not Otherwise Specified" or "NOS" disorders, whereby clinicians can diagnose the presence of a mental disorder (e.g., major depression) if the subject manifests sufficient impaired functioning without fulfilling full symptom criteria for that disorder. The latter two advantages are particularly important when considering possible cultural influences on the reporting of psychiatric distress by subjects (e.g., a tendency to report somatic complaints as described previously) that might otherwise be missed by completely structured interview questions and that might be expressed in lieu of traditional DSM symptom criteria. This data set's extraordinary nature is also highlighted by its rare combination of size, stratified random sampling, extremely high response rate, and sampling of both urban and rural samples.

A brief summary of the Phillips et al. (2009) study follows. This sampling frame included 113 million adult individuals, representing 12% of China's adult population. Multistage stratified random sampling methods identified 363 primary sampling sites in four provinces. Simple random selection methods identified 66,554 adults; 63,004 (94.7%) completed the first-stage screening (the 12-item General Health Questionnaire (GHQ)) supplemented by several items (Goldberg & Williams, 1988). Based on a combination of number of risk factors present and GHQ score reported, respondents were classified into three risk strata for mental illness: high-risk patients (17%), moderate-risk patients (17%), and low-risk patients (66%). Screening interviews were conducted in person by a trained psychiatric nurse; blinded re-interviews showed excellent reliability ($\kappa = .84$). For the second-stage assessment, all high-risk patients and a random selection of moderate- and low-risk patients were selected. Psychiatrists blind to the first-stage screening gave semistructured diagnostic interviews using the Chinese translation of the SCID. An extremely high percentage (16,577/17,598 or 94.5%) of the 63,004 screened patients assigned to the second-stage assessment completed the SCID. Blinded re-interviews for a random selection (15.6%) of interviews resulted in extremely high agreement (κ = .94 to .98) for any current or lifetime SCID diagnosis. Persons meeting criteria for any mental disorders reported any prior treatment (Phillips et al., 2009).

The study's main results indicated that 1-month prevalence of any mental disorder within China was 17.5% (95% confidence interval (CI), 16.6–18.5). However, 4.2% of the reported 1-month prevalence was attributable to "Not Otherwise Specified" disorders, meaning that the adjusted 1-month prevalence declined to 13.3% (95% CI, 12.4–14.1) after exclusion of NOS disorders. One key implication of this finding is that a substantial proportion (24%) of all diagnosable mental disorders within China were composed of culture-specific constellations of psychological symptoms that did not neatly fit criteria as defined by DSM. When considering separate disorders, the prevalence of mood disorders was 6.1% (95% CI, 5.7–6.6), that of anxiety disorders was 5.6% (95% CI, 5.0–6.3), that of substance abuse disorders was 5.9% (95% CI, 5.3–6.5), and that of psychotic disorders was 1.0% (95% CI, .8–1.1). A second main finding was that the reported level of help-seeking was remarkably low; only 8.2% of those diagnosed with a mental illness had ever sought professional help. However, differences in help-seeking emerged by diagnosis. Greater than 70% of patients with psychotic disorders had received professional help at some point, but more than 88% of those with non-psychotic mental illnesses had never received any type of professional help. The low level of help-seeking for non-psychotic disorders was attributed to cultural factors (e.g., interpretations that symptoms may signify something other than mental illness, or fear of severe stigma) and other systemic factors, such as unavailability of services due to cost, distance, or lack of social services (e.g., universal health coverage). To the degree that the low levels of psychiatric treatment are attributable to cultural factors within China, the extent of help-seeking among Asian Americans for non-psychotic disorders might also be expected to be relatively low compared with that of the US general population.

### *Immigration Processes and Psychopathology*

From the preceding landmark study, we understand that a substantial prevalence of mental illness exists in native Asian contexts such as China. Risk of developing psychopathology might then be further modified by processes that occur during immigration to the United States. Two alternative theories have been proposed for how immigration to the United States might influence psychopathology among Asian Americans (Hwang, Chun, Takeuchi, Myers, & Siddarth, 2005). Newly arrived immigrants may encounter multiple adverse circumstances, such as having to adjust to language barriers, low-paying menial jobs, and loss of social networks from the native context. These, along with related stressors with adapting to a new immigration setting, are conceptualized as *acculturative stress*, which might increase the risk of developing mental disorders among new immigrants to the United States. Alternatively, as immigrants become exposed to US norms, they may gradually take on characteristics of psychopathology experienced by the general US population (i.e., manifesting a higher prevalence of disorders because the US general population has typically exhibited higher prevalence of mental disorders compared with other ethnic minority groups, as described previously). This process of *cultural assimilation* implies that as culturally protective factors gradually erode with greater acculturation, risk of developing mental disorders slowly increases.

The developmental context associated with generation of immigration to the United States and psychopathology risk has been further advanced by Takeuchi, Hong, Gile, and Alegria (2007). These researchers conceptualized Asian American immigrants as belonging to different generations based on the age at which they arrived in the United States: generation 1.50 includes individuals who immigrated to the United States at 0–12 years of age; generation 1.25 (13–17 years); generation 1.0a (18–40 years); and generation 1.0b (41+ years). Risk of developing psychopathology is viewed as being heavily influenced by the developmental contexts in which an individual immigrates to the United States. For example, members of the 1.50 generation, or immigrants who arrived in the United States as children, receive much of their schooling in the United States, have better English language abilities, and are more able to grasp American culture and values compared with immigrants in the other generational categories. In addition, immigrants who arrive as children are more likely to have similar opportunities for mobility as their

American peers as well as opportunities to engage in risky behavior. Furthermore, generational differences in psychopathology may manifest due to the fact that the onset of many psychiatric disorders occurs in adolescence or early adulthood (American Psychiatric Association, 1994) and immigrants arriving at earlier ages consequently have a longer period of time in this risk period. This contextual framework proposes a more nuanced conceptualization by which to understand risk of developing psychopathology beyond prior crude classifications of immigrants as US born versus non-US born, an approach that characterizes many prior studies.

### *Diagnostic Methodologies and Impacts on Prevalence*

Central to the reliable and valid estimation of prevalence of psychiatric disorders among Asian Americans is a critical analysis of the assessment methods utilized for this purpose. While ensuring language equivalence of measures comprises a necessary first step, the translated measure must still demonstrate that it assesses the same underlying theoretical construct (i.e., that the measure exhibits construct validity). The critical risk of applying translated assessments to other cultural groups is the possible failure to account for culturally relevant emic constructs that are salient to the cultural group (Cheung, Cheung, & Zhang, 2004). In assessing psychopathology among Asian American groups, this risk is particularly salient as indicated by the Phillips' (2009) study, in which nearly one-fourth of identified cases of mental illness in China resulted from culture-specific manifestation and experiences of psychological symptoms.

Incorporating culture-specific assessments of psychopathology is especially relevant in the case of completely structured interview schedules, such as the WMH-CIDI. As described previously, the WMH-CIDI begins with a structured series of screening questions that lead to more in-depth probes if responded to affirmatively. If these structured screening questions do not encompass culturally relevant aspects of psychopathology, it is quite possible that substantial numbers of cases will be misclassified (i.e., they will be "false negatives"). Deep cultural knowledge of a group that becomes operationalized via culturally sensitive stem questions of interview modules may thereby significantly influence the accuracy and prevalence of identified psychiatric disorders (Lee, 2002).

Accordingly, in the NLAAS, Alegria et al. (2004) accounted for this important methodological consideration by systematically incorporating emic expressions of disorders into the CIDI. They first undertook extensive qualitative research to create one supplemental screening question for each of four disorders that entered subjects into specific diagnostic conditions. These supplemental probes were developed by querying respondents to suggest probes that signified comparable symptoms and by examining how the respondents interpreted the original screening questions. By identifying culture-specific concepts within each ethnic group, these investigators incorporated emic symptom expression not specified by DSM-IV criteria in identification of a psychiatric disorder. This key innovation further augmented the established methodological strengths of the CIDI, which includes acceptable reliability with the SCID for assessment of the prevalence of anxiety or mood disorders (Haro et al., 2006). Furthermore, the completely structured format of the CIDI allows administration by trained lay (i.e., non-clinician) interviewers, which is advantageous in the implementation of large-scale, and often quite expensive, psychiatric epidemiology studies (Dohrenwend et al., 1992).

In evaluating the main benefits of the SCID compared with the CIDI, the SCID offers the obvious advantage in detection of disorders by providing clinicians flexibility in querying symptoms. Furthermore, if respondents do not meet full criteria of a disorder but manifest significant functional impairment in the presence of several main symptoms congruent with the diagnosis, clinicians have the option of diagnosing the presence of a "Not Otherwise Specified" disorder. Clinicians using the SCID thus have the option to use flexible, semistructured probes in their local vernacular, therefore eliciting more in-depth information about symptomatology than is allowed by completely structured clinical interviews such as the WMH-CIDI (Haro et al., 2006). The semistructured interview format of the SCID thus allows clinicians (who are familiar with the local cultural context) to rephrase questions. As noted previously, allowing experienced clinicians from the local cultural context to ascertain whether an individual meets a specific symptom criteria facilitates culturally syntonic operationalization of DSM criteria, many of which necessitate at least some interpretation and clinical judgment during clinical interviewing (Kessler & Ustun, 2004). Furthermore, if the respondent's presentation is culturally congruent with a diagnostic category but he or she does not meet full criteria, the clinician may diagnose the presence of a NOS disorder. These features may be particularly important in the assessment of psychopathology among Asian American groups, where respondents due to cultural influences might experience or express psychological distress in nontraditional ways and because DSM-IV presumes universality of its diagnostic criteria with very little consideration to cultural variation (Mezzich et al., 1995). One main implication is that the semistructured SCID may be more appropriate to detect culturally nuanced manifestations of psychopathology that might be missed by the completely structured WMH-CIDI, thus potentially leading to identification of higher, and presumably more valid, estimates of prevalence of psychopathology. This includes the potential assigning of cases to NOS categories. Thus, it is our opinion that the SCID's ability to account for the way in which cultural prescriptions shape how distress is associated with mental illness (Lee, 2002) is a key feature that may provide a degree of ecological validity unlikely to be matched by structured, lay individual-administered interviews such as the WMH-CIDI.

### *Mental Health Service Utilization Studies*

Turning our attention to mental health service use among Asian Americans, to the extent that findings from Phillips et al.'s (2009) study in China are applicable, we might expect a lower rate of mental health service utilization among Asian American groups compared with White Americans. In addition, a prior review (Yang & Wonpat-Borja, 2006) reported that six of seven mental health service utilization studies based on non-population-based samples indicated that Asian American youth, adults, and elders used almost all types of mental health services to a significantly lesser extent compared with their Anglos counterparts both on the regional and the national level. These studies also demonstrated that the proportion of Asian Americans who utilized inpatient and outpatient mental health services was roughly one-third of the proportion expected based on their population size. Our current focus on mental health service utilization studies based on the NLAAS allows us to corroborate, disconfirm, or modify our understanding of help-seeking among Asian Americans from these prior studies. The advantages of the NLAAS over prior mental health service utilization studies include the fact that it is based on a national sample of Asian Americans that ascertained a wide diversity of mental disorders and that it included both Asian immigrants and US-born Asian Americans. In addition, the NLAAS examined help-seeking patterns by individuals who had a probable need for services (i.e., a DSM-IV diagnosis within the past 12 months) and those who had no probable need for services.

The main findings (Abe-Kim et al., 2007) indicated that among respondents overall, 8.6% sought help from "any service" (i.e., specialty mental health care, general medical care, or human service providers/alternative services including traditional healers) in the prior 12 months. Only 3.1% of respondents overall sought help from mental health providers. Importantly, the proportion of help-seeking endorsed differed by generation. US-born individuals used "any services" at significantly higher rates than did immigrants (12.7% vs. 7.4%), and they specifically demonstrated higher rates for specialty mental health care (6.2% vs. 2.2%). These differences were most pronounced in third or later generations; these individuals had the highest rates of use of "any services" (19.3%) compared to individuals who were first (7.4%) or second (8.1%) generation, as well as higher rates of specialty mental health care (10.1%) versus second-generation (3.5%) and first-generation (2.2%) individuals. Furthermore, use of "any services" was greater among individuals with a probable DSM-IV diagnosis (34.1%) during the past 12 months compared with individuals without a diagnosis (6.0%). Surprisingly, among respondents with a probable diagnosis, none of the following expected predictors were significantly associated with service use: whether US born or not, English language proficiency, years in the United States, specific Asian subgroup, or age at time of immigration. However, those who were third generation or later with a DSM-IV diagnosis during the past 12 months sought help from "any services" at higher rates (62.6%) compared with those who were first generation (30.4%) or second generation (28.8%). Lastly, most respondents across the four different Asian American ethnic groups reported "being satisfied" with the care they received from "any service" (72.1–92.2% across groups). Yet once again, those who were third generation or later most frequently endorsed that treatment helped "a lot" (81.1%), followed by US-born individuals (72.6%), with the lowest proportion among immigrant individuals (51.5%).

The main NLAAS findings appear to corroborate and significantly extend previous studies on mental health service underutilization among Asian and Asian Americans. In the NLAAS, only 8.6% of Asian Americans sought help from "any services" compared with 17.9% of the general population as reported in the NCS-R (Kessler et al., 2005), thus signifying treatment underutilization. This pattern of mental health service underuse persisted even among individuals with a probable DSM-IV diagnosis; 34.1% of such Asian Americans sought "any services" compared with 41.1% of all such individuals from the general population sample of the NCS-R (Kessler et al., 2005). It appears that degree of acculturation to US norms is central to predicting mental health service use among Asian Americans. Strikingly, third-generation Asian Americans were quite similar in their report of "any service" (19.3%) compared with the US general population sampled in the NCS-R (17.9%). In addition, increased age (particularly among Chinese and Vietnamese subgroups) was associated with a decrease in the probability of seeking mental health services (Nguyen & Lee, 2012).

Also noteworthy and unexpected was that characteristics such as English language proficiency were not associated with service use, thus indicating that specific cultural factors (e.g., fear of stigma or losing face) may hinder mental health service use above and beyond "generic" immigrant-based obstacles such as poor English language proficiency or paucity of knowledge regarding mental health services. This interpretation is supported by findings that perceived anticipated shame was associated with a lower probability of utilizing "any services" (Spencer et al., 2010). These "generic" immigrant barriers, instead of being associated with "formal" mental healthcare and general healthcare services as expected, appeared to be associated with increased use of "informal" services (i.e., defined in this case as religious or other traditional healers). Higher levels of perceived discrimination based on race/ethnicity combined with poorer English proficiency were found to be associated with greater use of informal services (Spencer et al., 2010). In summary, NLAAS findings indicated that Asian Americans evidence substantial mental health service underutilization compared with the US general population, that Asian Americans who are most acculturated to US norms utilize mental health services most frequently and on par with the US general population, and that culture-specific barriers such as anticipated shame appear in part to explain these patterns of underutilization.

## *Prevalence and Correlates of Psychopathology Within Asian American Groups*

Because of the focus of the NLAAS studies on substance abuse, anxiety, and major depressive disorders, we are able to evaluate findings regarding these disorders among Asian American groups in a substantive manner. We provide a more in-depth analysis of major depression due to the larger literature examining this disorder among specific Asian American subgroups. For all classes of disorders, we note prevalence rates among Asian American groups compared with the US general population. We next describe by disorder to what extent prevalence rates are found to vary by immigration status and gender—two sociodemographic variables that have been well studied in prior investigations. Our review excludes other disorders, such as eating disorders and personality disorders, because the NLAAS does not assess these disorders; however, we briefly summarize the existing literature on schizophrenia spectrum disorders among Asian Americans because these studies promise to inform the findings on mental health help-seeking underuse described previously.

### *Substance Abuse, Anxiety, and Major Depressive Disorders*

The main findings in the NLAAS (Takeuchi et al., 2007), utilizing the WMH-CIDI to ascertain prevalence among Asian Americans, indicate a lifetime prevalence rate of 17.9% of any disorder. Prevalence for specific classes of disorders includes 9.1% for any major depressive disorder, 9.8% for any anxiety disorder, and 4.0% for any substance disorder. These rates are far lower than the lifetime prevalence rates reported in the US general population (Kessler et al., 2005), which include 46.4% for any disorder,[1] 16.6% for any major depressive disorder, 28.8% for any anxiety disorder, and 14.6% for any substance disorder. This pattern also holds when considering 12-month prevalence rates among Asian Americans. The NLAAS indicates a 12-month prevalence rate among Asian Americans of 9.5% for any disorder, 4.7% for any major depressive disorder, 5.8% for any anxiety disorder, and 1.3% for any substance disorder. These percentages remain far lower than the 12-month prevalence rates found within the US general population of

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[1] Note that as discussed previously, this estimate of "any disorder" among the US general population includes the class of impulse control disorders, which the NLAAS excludes. However, this methodological difference does not appear sufficient to account for disparities in lifetime prevalence of "any disorder" between these two groups specifically, because lifetime prevalence of any impulse control disorder is estimated at 24.8% and 12-month prevalence is estimated at 8.9% among the US general population.

26.2% for any disorder, 9.5% for any major depressive disorder, 18.1% for any anxiety disorder, and 3.8% for any substance disorder.

When considering the effect of immigration status on prevalence among Asian Americans, it appears that being US born or arriving to the United States at an early age (i.e., age 12 years or younger) is associated with an increased risk of developing a mental disorder. These more acculturated Asian American groups had the highest lifetime rate of any disorder (25%) compared with other Asian American immigrant groups, who demonstrated lifetime prevalence rates of 13–15%. This general pattern also held when considering the specific classes of anxiety and major depressive disorders. Furthermore, regression analyses indicated that immigration at a younger age among Asian Americans was associated with greater risk for any disorder, any anxiety disorder, and any major depressive disorder compared with immigration at later ages. This pattern differed slightly when considering substance disorders, for which US-born respondents alone had the highest lifetime prevalence (13%) compared with other immigrant groups (with the lowest prevalence being <2% among first-generation immigrants). Overall, it appears that greater acculturation via either being US born or immigrating to the United States at an early age is associated with a higher risk of developing mental disorders among Asian Americans.

When investigating the influence of gender on psychopathology among Asian Americans, it is instructive to examine whether these effects parallel those found in the US general population. Female gender has traditionally been found to be associated with higher rates of anxiety and major depressive disorders, whereas male gender has been found to be associated with higher rates of substance disorders (Kessler et al., 2005). Because these gender effects were also reported in Phillips et al.'s (2009) psychiatric epidemiology study in China, there is reason to believe that these patterns might also persist within Asian American groups. When examining this relationship among Asian Americans overall, somewhat surprisingly, gender significantly predicted the probability of having a lifetime substance abuse disorder only. As expected, the risk among Asian Americans of developing a lifetime substance disorder for men was nearly four times greater than that for women. However, female gender was not associated among Asian Americans with greater likelihood of developing a lifetime anxiety or major depressive disorder.

One study (Jackson et al., 2011) investigating the lifetime prevalence of major depressive episode specifically among the four Asian American subgroups (i.e., Chinese, Vietnamese, Filipino, and "Other Asian") enables further examination of potential immigration and gender effects among the individual Asian American groups. The pattern that greater acculturation (as represented by being US born vs. being an immigrant) is linked with a higher risk of developing a major depressive episode was found among the Chinese American (21.5% among US born vs. 7.7% among immigrants) and the Filipino American (21.5% among US born vs. 7.7% among immigrants) subgroups specifically, with the proportions among Other Asians being roughly equivalent (10.2% among US born vs. 11.0% among immigrants; results are not available for the Vietnamese American group). When investigating the effect of gender on developing a major depressive episode among the specific Asian American groups, the proportion of females who reported a major depressive episode was higher among all of the subgroups compared with males, although this difference was statistically significant only among the Chinese American subgroup (12.6% among females vs. 7.2% among males). This suggests that nuanced gender effects for major depression, although not readily emergent when the Asian American group was examined overall, might more clearly emerge when examining the Asian American subgroups specifically. Interestingly, there also appeared to be an interaction between immigration and gender among the Chinese subgroup specifically, because female US-born Chinese Americans exhibited the highest proportion of major depressive episode (33.2%) among all Asian American subgroups, a proportion that appeared to be even slightly greater than that of US-born females (30.8%). This finding further underscores the importance of examining psychopathology prevalence among specific Asian American subgroups and identifying the underlying mechanisms that might result in increased risk of psychopathology among particular high-risk subgroups.

In summary, Asian Americans exhibit lower prevalence of lifetime and 12-month mental disorders compared with the general US population as assessed by the WMH-CIDI. However, as acculturation to the United States increases among Asian Americans (i.e., being US-born or immigrating before the age of 12 vs. other immigrants), rates of psychopathology also increase. Gender effects also emerge among Asian American groups but are more inconsistent. Among Asian Americans overall, gender exhibits expected effects in substance abuse and also shows expected effects among the Chinese subgroup for a major depressive episode only. Specific subgroups appear to have elevated risks of developing psychopathology, with US-born Chinese American women having a significantly heightened risk of developing a major depressive episode.

### *Schizophrenia Spectrum Disorders*

As noted previously, the NLAAS did not examine prevalence of schizophrenia spectrum disorders because the WMH-CIDI overestimates prevalence of psychosis in population samples. Here, we briefly discuss a recently emerging body of literature regarding schizophrenia spectrum disorders among Chinese Americans to illuminate possible factors underlying the underutilization of mental health services described previously. These studies illustrate the role that anticipated shame and stigma, particularly that associated with loss of face (Yang & Kleinman, 2008), might play in Asian Americans' decreased use of Western mental health services. For example, Chinese American community members endorse greater stigma toward Western psychiatric services compared with traditional Chinese medicine in the treatment of depression and schizophrenia (Yang et al., 2008). Furthermore, the formal diagnosis of schizophrenia is linked with increased stigma among Chinese community members (Yang et al., 2012) and Chinese American family members of individuals with psychosis (Yang & Singla, 2011). Alternative indigenous interpretations of the inflexible and suspicious thinking (i.e., "excessive thinking") associated with psychosis have been identified and are linked with decreased stigma among Chinese family members of individuals with psychosis (Yang et al., 2010). Stigma also exhibits culture-specific manifestations in Chinese immigrants because stigma among individuals with psychosis appears to be social network-based and to exhibit characteristics intrinsic to Chinese social organization (Chen, Lai, & Yang, 2013). These "culture-specific" aspects of mental illness stigma (Yang et al., 2007) also exert their most powerful effects by threatening to contaminate the lineage of Chinese Americans (Yang et al., 2013). This set of findings, although particular to schizophrenia spectrum disorders and Chinese American groups, serves as a basis to understand stigma and underutilization of mental health services for other psychiatric illnesses and for other Asian American ethnic groups as well.

### *Potential Mechanisms Underlying Generational Differences in Mental Disorders Among Asian Americans*

The previously discussed pattern of findings indicates that prevalence of mental disorders among Asian American groups is heterogeneous across differing subgroups. However, one relatively consistent finding is that increased acculturation to US norms, represented as being US born or immigrating to the United States before age 12 years, is associated with greater risk of developing mental disorders. In this section, we describe several possible mechanisms related to immigration, including gender effects, loss of subjective social status, and experience of discrimination, in an attempt to clarify some of the possible complex associations between immigration-related factors and psychopathology among Asian Americans.

#### GENDER DIFFERENCES AND IMMIGRATION CONTEXT

Takeuchi et al. (2007) found that Asian men and women differ in the association between immigration-related variables and mental disorders, suggesting that gender interactions with immigration context may influence risk of developing psychopathology. Among women, nativity was the most stable predictor of any lifetime depressive, anxiety, substance abuse, and psychiatric disorder, with US-born women having higher rates of most disorders compared with non US-born women. However, for men, nativity status (i.e., being US born) was primarily associated with increased lifetime substance abuse disorder. In addition, for men, it was found that those who spoke English well (excellent or good) were less likely to have any lifetime depressive, anxiety, or psychiatric disorder than were men who were less proficient in English. However, for Asian American women, English language proficiency was not associated with psychiatric disorders. These associations might signify contextual interactions with gender in the development of psychopathology because more proficient speakers of English may have a higher socioeconomic position in the United States (Takeuchi et al., 2007). English language proficiency may thereby serve as a marker for the ability of male immigrants in particular to move outside of their immediate social circles and expand their opportunities for employment and other types of social and economic resources, thus reducing their risk of psychopathology.

### SUBJECTIVE SOCIAL STATUS

Elevated risk of developing mental illness might result from a perceived decline in social status from the native context to the United States, with immigrants who perceive greater loss in social standing being at greater risk for developing psychiatric disorders. This follows traditional social theory that status inconsistency produces conflicting expectations and experiences that lead to frustration and uncertainty for the individual, thus increasing psychological stress (Dressler, 1988; Jackson, 1962). Upon analyzing the association between subjective social status (SSS) and mental health disorders among immigrants to the United States, Nicklett and Burgard (2009) found that a decline in SSS, or, "the individual's perception of his own position in the social hierarchy" (p. 569, Jackman & Jackman, 1973), puts immigrants at increased risk of major depression. In Nicklett and Burgard (2009), immigrants' reports of what their social standing had been in their countries of origin were compared with their perceived current standing in the United States. Even when logistic regression models were used to control for a variety of sociodemographic and immigration-related characteristics, a significant perceived decline in subjective social status was found to be associated with an increased risk of a depressive episode (odds ratio, 3.0; 95% CI, 1.3–6.6). These findings suggest that immigrants who experience downward social mobility are at elevated risk of major depression. Nicklett and Burgard's results thus identify psychological and contextual processes that may influence the mental health of specific groups of immigrants in nuanced ways.

### ACCULTURATIVE STRESS, DISCRIMINATION, AND PSYCHOPATHOLOGY

Yet another immigration-related factor that might influence the development of psychopathology is acculturative stress. In a recent study, DeVylder et al. (2013) examined the association between acculturative stress and psychotic-like symptoms among Asian American immigrant groups. As described previously, acculturative stress refers to the tension associated with the acquisition of an additional culture that may have detrimental effects on mental and physical health (Rudmin, 2009). As Asian American immigrants adjust to their new lives in the United States, they may struggle to adapt to the sets of values and social norms specific to American culture while maintaining the culture of their home country. The stress of this cultural learning process may contribute to the risk of psychosis.

DeVylder et al. (2013) examined a sample of first-generation Asian American participants using the NLAAS. Acculturative stress was measured through a nine-item dichotomous acculturative stress survey taken from Guarnaccia et al. (2007). Sample items measuring acculturative stress included difficulty with interaction due to language barriers, fear of deportation, and limitations of contact with friends and family. Lifetime prevalence of psychotic-like experiences (PLEs) was assessed using the WHO-CIDI 3.0 psychosis screen (Kessler & Ustun, 2004). Symptoms included visual hallucinations, hearing voices, and delusions. The main findings from the study indicated that the more acculturative stress items endorsed, the greater the risk for lifetime PLEs, particularly visual and auditory hallucinations. This particular finding illuminates one potential underlying mechanism associated with immigration and the development of Asian American psychopathology.

Another key immigration-related factor that might increase the risk of psychopathology is race-based discrimination because time of immigration to the United States results in different opportunities to encounter discrimination and might also shape the subjective impact of discrimination. Utilizing data from the NLAAS, Gee, Spencer, Chen, Yip, and Takeuchi (2007) examined the association between perceived discrimination and mental health among Asian Americans. Perceived discrimination was measured by nine items assessing perceptions of everyday discrimination (Williams, Yu, Jackson, & Anderson, 1997). The scale ranges from 1 to 5 and indicates whether an individual perceived discrimination in a range from *almost every day* to *less than once a year.* Some examples of everyday discrimination experiences include experiencing less courtesy, less respect, poor service, being thought of as not smart, other people being afraid of the respondent, being thought of as dishonest, being thought of as not as good as other people, being insulted, and being threatened/harassed. Higher scores on this measure represented higher levels of perceived discrimination. The main findings showed that self-reported racial discrimination is associated with greater odds of having any DSM-IV disorder, depressive disorder, or anxiety disorder within the past 12 months. Furthermore, this relationship is not explained by social desirability, physical health, other stressors, and sociodemographic factors. These two studies are especially important to consider in the context of the findings that more US-acculturated Asian Americans tend to have higher risk of psychopathology because length of time in the United States might also result in more opportunities to experience acculturative stress as well as race-based discrimination.

## Cultural Neuroscience and Population Mental Health

Although global mental health has made notable advances in methodology and sampling, social neuroscience provides a new approach by which to understand variations in prevalence of mental disorders across different populations. In particular, cultural neuroscience may play a powerful role in explaining cultural variations in the expression and manifestation of mental health disorders. Adopting a cultural neuroscience approach might provide a better understanding of how cultural context influences normal brain functioning and would also provide the ability to examine the neurobiological underpinnings of mental disorders. Recent studies utilizing fMRI give insight into how neuroscience can be a powerful methodological tool in mental health research among ethnically diverse groups. One potential avenue is to examine the biological substrates underlying race-based discrimination because increased discrimination was shown to be associated with greater risk of psychopathology among Asian American groups (Gee et al., 2007). Examining the underlying brain regions that are activated by discriminatory experiences, if these regions are found to be linked with neurological processes of psychopathology, may provide insight into how discrimination may predispose or exacerbate psychopathology within different groups. For example, fMRI studies examining discrimination among ethnic minority groups have found increased activation of the insula when African American respondents perceived social exclusion as attributable to their race (Masten, Telzer, & Eisenberger, 2011). Social exclusion effects are also exaggerated and/or longer lasting in bipolar disorder (Gratz et al., 2012), schizophrenia (Perry, Henry, Sethi, & Grisham, 2011), and social anxiety (Zadro, Boland, & Richardson, 2006), with associated areas of increased anterior cingulate cortex and insula activity and decreased ventral prefrontal cortex activation linked with social exclusion-induced distress (Masten et al., 2011; Maurage et al., 2012). Although no neuroscience links between discrimination and impacts on psychopathology have yet to be examined, we suggest this area as potentially generative in investigating how cultural context might shape experience of mental disorders in different groups.

Another intriguing area in which cultural neuroscience might contribute to understanding cross-cultural variation in psychiatric disorders is in the differing distributions of certain genotypes that have been found to be associated with specific mental disorders. Investigations in this area have been made possible by gene × environment interaction studies that have demonstrated genetic linkages with higher risk of developing major depression. The traditional gene × environment model of depression proposes that those who carry the short variant of the serotonin transporter gene (*5-HTTLPR*) who encounter greater stressful life events, compared with those who carry the long allele, evidence higher risk of developing major depressive episodes (Caspi, Hariri, Holmes, Uher, & Moffitt, 2010; Caspi et al., 2003). However, certain racial groups, particularly those from East Asia, possess the short allele of the serotonin transporter gene in greater proportions (Hairiri et al., 2002). According to the traditional gene × environment model, this differing proportion of the short allele of the *5-HTTLPR* gene in populations should then have direct implications for the prevalence of depression found across groups. However, this topic has yet to be systematically investigated; thus, it represents an area of tremendous future opportunity.

In summary, we have provided an overview on how mental disorders may differ by ethnic group within US population studies. Utilizing Asian Americans as a case example, we detailed how local metaphors as culturally mediated forms of distress shape manifestation of psychopathology, critiqued how varying diagnostic methodologies differ in their definition of psychopathology and thereby may influence estimates of prevalence, and evaluated how prevalence of mental disorders differed within Asian American groups utilizing a landmark study within China to inform our interpretations. We then outlined several possible mechanisms that might underlie cultural differences in psychiatric disorders among Asian Americans, an area in which cultural neuroscience may be especially useful as a new perspective and method. We intend this synthesis of research to provide a foundation by which to investigate key biological processes that may underlie variations in psychopathology across diverse cultural groups and to inform how cultural neuroscience may spur further innovation in research in population mental health.

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## CHAPTER
## 23

# Culture, Genes, and Socioemotional Neurodevelopment: Searching for Clues to Common Mental Disorders

Joanna Maselko

**Abstract**

The country, or even region, in which an individual is born is a significant determinant of risk of developing a neuropsychiatric disorder. Differences in risk of developing a disorder are closely tied to the overall burden of neuropsychiatric disorders in a given population. Using age-standardized disability-adjusted life years (DALYs) per 100,000 inhabitants as a measure of disease burden, the World Health Organization (WHO) estimates that neuropsychiatric disorders are responsible for 10–15% of disease burden worldwide, with unipolar depression and alcohol disorders making the largest contributions. WHO estimates that the burden of unipolar depressive disorder ranges from 315 DALYs per 100,000 in China to 1235 DALYs in Cuba and 1651 DALYs per 100,000 in the United States. Similar patterns have been documented with other disorders, such as anxiety and schizophrenia. Variation in disease burden remains even after accounting for varying definitions of mental health and sources of data.

**Key Words:** culture, neurodevelopment, global mental health disparities, neuropsychiatric disorders, age-standardized disability-adjusted life years

## Cultural and Geographic Variation in Disease Prevalence and Risk

A key finding in the study of global mental health disparities is that the country, or even region, in which an individual is born is a significant determinant of risk of developing a neuropsychiatric disorder (Kieling et al., 2011; Lund et al., 2011; Prince et al., 2007). Differences in risk of developing a disorder are, in turn, closely tied to the overall burden of neuropsychiatric disorders in a given population. Using age-standardized disability-adjusted life years (DALYs) per 100,000 inhabitants as a measure of disease burden, the World Health Organization (WHO) estimates that neuropsychiatric disorders are responsible for 10-15% of disease burden worldwide, with unipolar depression and alcohol disorders making the largest contributions (Murray & Lopez, 1996; WHO, 2002). As an example of the variation of the burden, WHO estimates that the burden of unipolar depressive disorder ranges from 315 DALYs per 100,000 in China to 1235 DALYs in Cuba and 1651 DALYs per 100,000 in the United States (WHO, 2002). Similar patterns have been documented with other disorders such as anxiety or even schizophrenia, which until recently was thought to have the same prevalence worldwide. Importantly, variation in disease burden remains even after accounting for varying definitions of mental health and sources of data (Hinton & Lewis-Fernandez, 2011; Prince et al., 2012; Sousa et al., 2010). In part due to our evolving thinking about cross-cultural definitions of specific neuropsychiatric disorders, the term “common mental disorder” (CMD) is sometimes used to refer to the most common types of mental health problems present in a population (Chandra & Satyanarayana, 2010; Patel, Kirkwood, Pednekar, Weiss, & Mabey, 2006; Servili et al., 2010). Throughout this chapter, the terms CMD and neuropsychiatric disorders are both used.

A growing body of multidisciplinary scholarship has explored putative reasons to explain the observed geographic variation in mental health disease burden (Prince et al., 2007), and two broad sociocultural pathways are especially relevant to cultural neuroscience. One hypothesis is that poverty and the harsh and stressful environment that it creates are key drivers of CMD rates. This hypothesis is supported by very robust evidence that, at the individual level, poverty is associated with higher risk of almost all mental health problems, including suicide (Jenkins et al., 2008; Maselko & Patel, 2008; Patel, 2001; Patel et al., 2006). The link between poverty and mental health is most strongly visible within countries, which is the level at which the meaning of "poor" and hence the mechanisms of poverty are thought to be most salient (Patel, 2001). The stark socioeconomic disparities in risk of developing a neuropsychiatric disorder, and its prognosis, are the drivers of much of the research presented in this book. A second hypothesis points to rapid economic development and the stresses and adaptation demands placed on individuals in quickly changing societies. Those who cannot quickly adapt to the new socioeconomic opportunities and are left behind are at highest risk, and they are presumably at even higher risk if they had remained poor in the absence of quick economic development. This hypothesis is supported by evidence that the total burden of neuropsychiatric disorders such as schizophrenia tends to be lower in "traditional" cultures versus the more "modernized" ones (Isaac, Chand, & Murthy, 2007; Raguram, Raghu, Vounatsou, & Weiss, 2004; Watters, 2011). These two hypotheses are ultimately complementary, and both invoke the stress pathway in which an individual's risk of CMD is shaped by his or her ability to successfully adapt to, and negotiate, the demands of his or her environment. The poverty hypothesis emphasizes the sheer harshness of an environment in poverty, whereas the modernization hypothesis suggests a type of mismatch between an individual's early life environment and the new one. In both scenarios, specific adaptations are needed to reduce risk of mental health problems.

## Developmental Origins of Disease

While we increase our understanding of which features of the sociocultural environment are most important for mental health, a consensus has emerged that experiences in the first few years of life are crucial in shaping risk of neuropsychiatric disorder later in life. Combining information from genes and on input from the external, social, and physical environment, the developing brain lays the foundation that shapes the developmental trajectory for the rest of the life course (Heim & Binder, 2012; Shonkoff, Boyce, & McEwen, 2009). This process of the embodiment of the environment relies heavily on epigenetic mechanisms such as methylation, which alters gene transcription and, in turn, an individual's phenotype and specific behaviors (discussed in more detail later) (Roth & Sweatt, 2011; Toyokawa, Uddin, Koenen, & Galea, 2012). A better understanding of the early life origins of disease has significant basic science and policy implications for those who are interested in ameliorating health disparities (Shonkoff et al., 2009) because this will inform the design of preventive and treatment interventions as well as the restructuring of the overall early physical and social environment in which children grow up (to the extent that it is malleable).

How the early life sociocultural environment impacts an individual's neurodevelopmental trajectory, and hence risk of neuropsychiatric disorder, is the focus of this chapter. The first section discusses the key theories of developmental neuropsychology that help us understand how the early environment becomes embodied, calibrating the nervous system in a way that may determine an individual's risk or resilience to mental health problems over his or her life course. This includes a discussion of "adaptation" from both the evolutionary and the psychological perspective. The chapter then discusses the possibility of mismatch between this calibrated system and the later environment and how the mechanism of differential sensitivity to the environment is an evolutionary response to this possibility. The section on parenting behaviors attempts to apply these models to this highly salient and cross-culturally diverse early childhood set of environmental inputs. The chapter concludes with a return to biological mechanisms with a discussion of genes, parenting, culture, risk, and the many unanswered questions remaining. Throughout, I attempt to include relevant cross-cultural literature to shed light on how some of the processes may operate differently in diverse environments.

In the past decade, two strands of research have emerged that inform our discussion. The first focuses on the role of "stress" in early life. Whereas initial studies documented the negative effects of early life stress (stress diathesis model), recent work has focused on the positive role that mild to moderate stress can have, suggesting a U-type relationship between severity of stress exposure early in life and later vulnerability to mental health problems (Del Giudice, Hinnant, Ellis, & El-Sheikh, 2012). This idea is sometimes referred to as the stress inoculation theory and is also the basis of the adaptive calibration model (ACM) (Del Giudice, Ellis, & Shirtcliff, 2011; Del Giudice et al., 2012). The second area of study has revealed that there is significant variation in the level of sensitivity to the social environment, including the previously mentioned stressors, between individuals (Ellis & Boyce, 2011). Influenced by genes and the social context, the research on differential susceptibility to the environment suggests that the sensitivity is "for better or worse" in that individuals who are sensitive are at higher risk of disorder given very negative early life exposures but also exhibit the best outcomes if raised in very supportive environments (Ellis, Boyce, Belsky, Bakermans-Kranenburg, & van Ijzendoorn, 2011). These two research strands are complementary and best understood within a broader evolutionary framework. They also form a very productive scaffolding for cultural neuroscience research from a developmental perspective.

## Using Early Life Environmental Input as Predictors of Future Environment

Beginning prenatally, the developing brain uses inputs from the internal and external environment to predict the future adult environment, and it "wires" itself accordingly (Laurent et al., 2013). In other words, the human brain has the ability to modify its developmental trajectory in an effort to match the anticipated future social and physical environment (Del Giudice et al., 2011). Models such as the biological sensitivity to context (BSC) and the ACM delineate some of the specific mechanisms underlying this dynamic process of environmental input and developmental trajectory(Boyce & Ellis, 2005; Del Giudice et al., 2011). These models are based on observations that early life experiences appear to be correlated with how responsive individuals are to their adult environments, specifically in terms of stress reactivity (usually measured by hypothalamic–pituitary–adrenal (HPA) axis reactivity). The most robust findings have been that children and adults exposed to abuse or other early life adversity have a very reactive stress response, as measured by HPA axis reactivity in response to a controlled stressor (Essex et al., 2011; Glover, O'Connor, & O'Donnell, 2010; Shea, Walsh, MacMillan, & Steiner, 2004). Initial studies such as these supported the idea that the developing brain has an evolved ability to filter and decipher environmental input and use this information to calibrate future response to stressful stimuli (Boyce & Ellis, 2005; Del Giudice et al., 2011). Furthermore, due to research among families "in the normal range," there is evidence that children who grow up in either very supportive or very harsh environments tend to have the highest levels of HPA axis reactivity in response to even mild stressors as adults (Belsky & de Haan, 2011; Gunnar, Frenn, Wewerka, & Van Ryzin, 2009). Empirical support for this idea is growing: For example, a study by Gunnar and colleagues divided 10- to 12-year-old children into three groups according to early life experiences surrounding adoption and foster care experiences. Children who grew up with biological parents and children who were adopted late from orphanages represented the low and extreme early life stress groups, respectively. Children who were adopted early and had lived with foster parents were the middle stress category. When the children were exposed to a mild stressor (Trier Social Stress Test for Children), the researchers observed a U pattern in terms of cortisol reactivity in that the reactivity was the same (high) for the low and severe stressor groups while being relatively diminished in the mild stressor group (Gunnar et al., 2009). Findings such as this supported the idea that harsh or very good settings calibrate the developing brain toward higher levels of responsivity to environmental input: for protection in the harsh environment and to take advantage of available resources in the good environment. Presumably, early neutral or inconsistent environments were deemed not as informative and responsivity was downregulated. We might expect that certain environments are more or less likely to generate consistent input, for example, if a child is being raised by multiple caregivers or if there is frequent migration. Although most studies show a positive association between a strongly reactive HPA axis and increased risk of mental health problems, it is not clear what level of reactivity is optimal or whether a highly reactive HPA axis should be considered dysregulated or not (Buitelaar, 2013). The answer likely is dependent on the specific nature of the stressor being responded to and the supportive nature of the social and physical environment. The findings related to stress responsivity can be extrapolated to other phenotypic attributes: The observed adult phenotype of an individual is the result of a calibration process using inputs from that individual's early years of life.

## Why Does This Happen? Evolutionary and Developmental Perspectives on Adaptation

The capacity to alter one's neurophysiological profile has evolved because there is no single best phenotype or strategy given diverse and changing environmental conditions: Diverse responses are needed. This leads to the intriguing idea that a much wider range of phenotypic traits (e.g., in hostility) than previously thought might be within the "normal" adaptive range and not inherently pathological. Furthermore, if a health disparities researcher is only working within one relatively homogenous cultural group, a behavior might be misclassified as "extreme" even though it is, in fact, perfectly normal and well within the evolutionary repertoire of adaptive behaviors. The use of the term "adaptive" at this point may diverge between adaptive strictly in the evolutionary sense and adaptive for a particular individual in his or her situation from a more psychological perspective (Frankenhuis & Del Giudice, 2012). For example, a hostile personality in reaction to a harsh environment may increase average fitness but may do so at the expense of that individual's mental health. In other words, an adaptive response (hostility) may be associated with an undesirable outcome (neuropsychiatric disorder), but this does not mean that the response is pathological in itself. It would not be correct to assume that a negative early environment derailed normal development by leading to hostility and increased risk of psychopathology, even as the hostility does increase psychopathology risk. We must be open to the idea that low hostility in a harsh environment is itself maladaptive and, on average, might be associated with increased mortality, which would preclude the development of a neuropsychiatric disorder (Meaney, 2001). Hostility is then the by-product of trying to "make the best of a bad situation" (Boyce & Ellis, 2005; Ellis & Boyce, 2011). It is not necessary to resort to the extremes of a "harsh" versus "good" environment to see differences in whether a specific phenotype increases risk of mental health problems because such differences occur cross-culturally. For example, a study of child characteristics among children in China and Canada revealed that shyness was linked with low peer acceptance among Canadian children but not Chinese children (Chen, Rubin, & Sun, 1992). This difference reflects both the different cultural meanings of "shyness" (fearful vs. cautious) and their potential mental health consequences through the pathway of social isolation and rejection (Chen, DeSouza, Chen, & Wang, 2006). In order to understand the role of the sociocultural environment in shaping the developmental trajectory, the distinction between a phenotype that is a result of a normal adaption and a maladaptive outcome is crucial (Frankenhuis & Del Giudice, 2012). This is especially so when using cultural neuroscience to understand mental health disparities because (1) the meaning and evolutionary adaptability of a given phenotype in a specific cultural context may not be easily understood and (2) attempts at changing the phenotype may be misguided and place an individual at higher risk if a new mismatch is created. What is adaptive and correlated with positive mental health in a developed, rich country setting may not confer the same long-term benefits in a low resource, developing context.

The life history (LH) theory provides a helpful lens through which to interpret the adaptive nature of specific phenotypes and behaviors. An organism's LH strategy refers to a developmental schedule (fast vs. slow) and the corresponding allocation of resources such as energy and time to specific activities, usually related to reproduction (Del Giudice et al., 2011). Whether an individual takes a faster versus slower trajectory is based on input from the environment. In general, harsh or unpredictable environments, in which risk of mortality is high, speed up the LH so that the individual has a chance to reproduce before dying (Del Giudice et al., 2011; Frankenhuis, Gergely, & Watson, 2013). Hence, early sexual debut, reproduction, and higher fecundity could simply be a response to the unfavorable environmental conditions. Obviously, this perspective is not new to cultural anthropologists, but it does offer another lens through which to connect evolutionary adaptation, a given "undesirable" phenotype, and risk of psychopathology. Conversely, a safe environment sends the signal that life might be longer and hence developmental milestones are relatively delayed. The LH hypothesis is further supported empirically through experimental studies on animals that confirm that negative early life exposure accelerates reproductive development (Frankenhuis et al., 2013). The difference in LH speed also represents the quantity versus quality trade-off and the "live fast, die young" approach.

### *Risk of Mismatch*

The LH trajectory and future stress reactivity are based on early life input. However, any developmental strategy may become maladaptive when (1) it is a risky strategy; (2) the environment changes between early life and adulthood; or (3) the prediction, which was based on probability, turns out to be wrong (Frankenhuis & Del Giudice, 2012). The risky strategy is uniquely maladaptive because of the increased likelihood of mortality prior to reproduction, whereas a mismatch to the environment requires the now adult brain to adapt anew in order to succeed. The potential for environmental mismatch has always existed because the developing brain relies on a statistical sampling of environment inputs and is, by definition, relying on incomplete information when calibrating itself for the anticipated future. Due to the rapidly changing nature of societies in the past century, as measured by increasing life expectancies, shifts from physical to more sedentary labor, to increased communication technologues, the likelihood of the input used for laying down the developmental trajectory not matching the adult environment seems especially high.

### *Logic of Differences in Sensitivity*

Because of the less than reliable nature of early life environment input in being adaptive, individuals vary in their sensitivity to these inputs (Ellis & Boyce, 2011; Ellis et al., 2011). Popularized by the research findings related to the serotonin reuptake inhibitor gene polymorphism (Caspi, Hariri, Holmes, Uher, & Moffitt, 2010), the concept of differential susceptibility to the environment puts forth the idea that individuals inherently vary in their level of sensitivity to the environment (Ellis et al., 2011). Sensitivity to environmental input in the specific developmental context refers to the extent that the longer-term developmental trajectory of an individual is affected by a given environmental stimulus experienced early in life. These differences in sensitivity are initially programmed genetically, and the final phenotype emerges as a result of gene–environment interactions and epigenetic modifications. Ellis and colleagues (2011) propose several key features of the differential sensitivity theory: (1) The sensitivity is to the social and physical environment with no innate distinction between "good" or "bad" environment; (2) higher levels of sensitivity lead to more pronounced changes in an individual's developmental trajectory directly tied to the environmental input; (3) the mechanisms involved in the "embodiment" of the environmental input are neurobiological and genetic; (4) polygenic variation is a strong determinant of how sensitive a given individual is to environmental input; (5) the degree of sensitivity is expected to vary across the life course in addition to across individuals; (6) the inherent variation in sensitivity across populations has evolved as an adaptive mechanism to diverse and changing environments; and (7) in summary, this variation is a key mechanism in the overall impact of the environment on an individual over his or her entire life course. By definition, this results in varying developmental trajectories between individuals even if they are exposed to the same environmental conditions (Ellis et al., 2011, pp. 7–8).

Most of the extant research on sensitivity to the environment has focused on understanding how various degrees of sensitivity can be adaptive or maladaptive. In this context, sensitivity to the environment is usually defined as the level of arousal and HPA axis activation in response to an environmental stressor (Meaney, Szyf, & Seckl, 2007). For example, an event such as an important exam or work presentation would lead to higher HPA axis arousal in someone who is sensitive, which can, in turn, increase focus and attention. On the other hand, an individual might be better off being immune to the social context when in a stressful competitive situation, when going against social convention is beneficial, or when he or she is engaging in a high-risk behavior. In these instances, one's performance might be improved by not being concerned about, or even aware of, what others are thinking (Del Giudice et al., 2011).

Del Giudice and colleagues proposed the Stress Response System (SRS) as the internal mechanism that either filters or amplifies incoming input based on a combination of prior input and genetic disposition (Chen et al., 2006; Del Giudice et al., 2011). The importance of the prior input is weighed heavily on input from the first few years of life and is the result of a continuous process of conditional adaptation. Del Giudice emphasizes that children are nudged onto different trajectories as a result of a combination of how sensitive they are and the environmental input. The process is continually calibrated and ultimately leads to a particular LH strategy. Sensitivity to these early cues determines how well matched/calibrated the individual is to his or her current environment. For example, a positive and nurturing early environment combined with a sensitive genotype is expected to result in a very sensitive individual. This person's SRS amplifies social inputs. If the environment continues to be positive, or at least within the person's ability to cope, this increased sensitivity enhances social learning through increased susceptibility and understanding of social feedback, activates cognitive domains associated with processes such as memory and attention to detail, and improves social bonding and relationships. This increased "information openness" is especially adaptive when the information is itself not damaging. On the other hand, this openness to social information comes at a high cost if the SRS amplifies environmental inputs that then overwhelm or surpass the individual's coping mechanisms. For example, such an individual might be overly sensitive to critical social feedback or vulnerable to being manipulated; he or she might also be easily distracted and have difficulty focusing in very busy environments (Del Giudice et al., 2011; Ellis et al., 2011). Whether the SRS ultimately has a function of filtering versus amplifying environmental input is a result of both genotype and early life environment. The mechanism through which the SRS becomes calibrated to either muffle or amplify environment input likely relies heavily on the process of DNA methylation. Using animal models, researchers have shown that early life adversity during sensitive periods increases methylation in specific genes (Roth & Sweatt, 2011). This relatively stable epigenetic process has the effect of "inactivating" a specific part of a gene by preventing its transcription. This hypermethylation process has been observed in several genes in the rat brain as a direct result of variation in a mother's licking and grooming and arched-back nursing behaviors (Weaver et al., 2004). Studies of suicide victims are also suggestive in linking early life adversity with hypermethylation (Labonte et al., 2013). Intriguingly, there is also evidence that some of the epigenetic changes can be reversed through changes in behavior or pharmacological manipulation (Roth & Sweatt, 2011).

The majority of the research so far has relied on a somewhat simplistic definition of the "early environment" in categorizing it along the spectrum ranging from harsh and abusive to positive and supportive while the main adult phenotype of interest has been the degree of sensitivity or reactivity to "stress." This is, of course, a gross oversimplification because there are likely hundreds, if not thousands, of phenotypes that are calibrated with early life environmental input. This provides a very exciting opportunity for cultural neuroscience to add to the understanding of how early life experiences impact later adult phenotypes and how culture ultimately "decides" whether these traits are adaptive or not.

## Where Does All of This Input Come From? Parenting and Culture

So far, this chapter has argued that the early developmental period is of crucial importance to our understanding of risk of common mental disorders. We have described relevant theoretical frameworks, rooted in evolutionary theory, that describe how early life experiences are used by the developing brain as data points toward predicting a future environment. Phenotypic differences among individuals emerge as a result of (1) the types of environmental input and whether this input suggests a "safe" or "unsafe" environment, (2) the (in)consistency of given input, (3) one's biological sensitivity to that input as partially determined by genotype, and (4) timing in the life course when the individual is exposed to given input. We have only briefly discussed what is meant by environmental input and how exactly this input is determined by culture. A focus on parenting provides this necessary step.

The most obvious nexus for culture meeting neuroscience in the context of development is the early parent–child relationship. There is a vast anthropological and psychological literature documenting cultural differences in parenting practices that logically dovetails with the literature showing cultural differences in neuropsychological processes emerging in childhood (Bornstein, 2002, 2012). Parents want what is best for their children: Culture "suggests" what is adaptive, and this is what is transmitted by parenting. The caregivers, other adults, and overall home environment together represent the developmental niche in which a child grows (Super & Harkness, 2002). The presence of the developmental niche ensures that features of the social environment, and the inputs they generate, become permanent at the neural level. Parental (or caregiving) behaviors are then the key mechanisms through which this process occurs. Specific norms, such as concerning what are and are not acceptable expressions of emotion, are presented repetitively, in varying contexts (Super & Harkness, 2002). The level of stability in these inputs additionally provides information about how predictable or not the environment is (which as described above, likely has independent neural effects). As children mature into adults, their caregiving environments are to a large extent responsible for the observed cross-cultural differences in neuropsychological processes between them (Bornstein, 2012).

### *Individualism Versus Collectivism*

A recurring theme in cultural neuroscience is one of individualism versus collectivism (Chiao & Blizinsky, 2010; Chiao et al., 2010; Tamis-LeMonda et al., 2008). When applied to parenting, these two value systems are translated to encouraging the development of autonomy versus relatedness in children (Tamis-LeMonda et al., 2008). These two domains are best seem as complementary and not opposite and are both present in many theories of child development (Keller, 2003). For example, attachment theory emphasizes the security that the parent relationship provides, which in turn enables the more autonomous exploration of the environment (Bowlby, 1969, 1973, 1980; Tamis-LeMonda et al., 2008). Parents in all cultures negotiate these values, trying to impart the correct balance that will give their child the best chances in life; in other words, parents try to shape their children's development with an eye toward predicting their adaptation in some future environment, within the constraints of their particular culture. Hence, with globalization and rapid economic development, what parents perceive as ideal is likely to change more quickly than it has in the past.

Culture seems to influence both the domains in life in which individuals are expected to be more autonomous versus relational as well as the overall balance of one to the other. One example is the comparison between paid work, where being very autonomous may be optimal, and family membership, where a collective and relational approach is most desired. Furthermore, based on what we are learning about the influence of specific genotypes, it seems likely that an individual's genotype may be yet another contributor to his or her overall preference in the balance of relatedness and autonomy.

In order to understand how cultural constructs such as individualism/collectivism and the more individual characteristics of autonomous/relational become etched in the brain, a focus on more proximal parental behaviors is needed. As mentioned previously, there is a large literature comparing specific behaviors across cultures, but there is also a growing literature that connects normal variation in parenting with neuropsychological indicators or outcomes (Bornstein, 2012).

### *Physical Contact*

There is a large taxonomy of specific parental behaviors and features of mother–child interactions that have been linked with child outcomes. The amount of physical body contact between an infant and an adult caregiver is probably the behavior for which there is the most research on both cross-cultural variation and links with neuropsychological indicators. In some places, infants rarely are not held by (or strapped to) a caregiver, whereas in others, infants spend much of the day without physical interactions with caregivers (Heidi Keller, Borke, Yovsi, Lohaus, & Jensen, 2005). The term "bodily contact" thus broadly includes things such as sleeping location (with parents vs. alone), normal mode of transport (e.g., on body vs. in stroller), and how much time an infant spends in skin-to-skin contact with a caregiver. This parental behavior is linked to developmentally salient interactions such as how long an infant cries before he or she is attended to and how well an infant is synchronized with maternal cues (Bigelow & Power, 2012). These interactions have in turn been associated with various neurophysiological outcomes, such as markers of HPA axis activation or reactivity. For example, several studies suggest that infants who are held more have lower cortisol levels and/or reactivity (Elverson, Wilson, Hertzog, & French, 2012). There is also some evidence that infants with more skin-to-skin contact with their mothers responded earlier (at 1 month vs. 2 months) to the mom's still face procedure, which the authors interpreted as faster development in terms of interacting with the mother (Bigelow & Power, 2012). Sometimes such findings are interpreted as showing the "protective" effect of skin-to-skin contact, but given all of the evidence presented here, this is not definite. The direction of the relationship between a specific parenting behavior and an outcome can depend on the sensitive period that is being observed and the specific pairing of the behavior/outcome. For example, it is unclear whether a stressed infant who is quickly soothed by the caregiver and exhibits a lower stress reaction (Gray, Miller, Philipp, & Blass, 2002) is more likely to become resilient through mechanisms of secure attachment and support or more vulnerable to future stress because he or she is not "inoculated" to stress.

Other related behaviors that have been studied in this context include co-sleeping/bed sharing (Tollenaar, Beijers, Jansen, Riksen-Walraven, & de Weerth, 2012; Welles-Nystrom, 2005; Worthman & Brown, 2007) and feeding behaviors (including Breast-feeding) (Binns, Lee, & Medimond, 2013; Sakashita, Inoue, & Kamegai, 2004; Santini et al., 2008; von Normann, 2009), with the majority of studies reporting null or protective findings with various psychological outcomes.

From a health disparities perspective, it is not obvious which parenting strategies that correlate to specific neurocognitive functions are adaptive versus not in that particular setting. For example, a study by Bornstein et al (2008) compared interactions of mother–child dyads from Italy, the United States, and Argentina in rural and urban areas. One of the findings was that across all three countries, women from rural areas were more intrusive than those from urban areas. In some contexts, intrusiveness may be associated with negative mental health outcomes and less than ideal development, but this cannot be said about women in Italy or Argentina without testing such a hypothesis empirically. A systematic review comparing parenting differences based on a family's majority versus minority status (Mesman, van Ijzendoorn, & Bakermans-Kranenburg, 2012) suggests that observed differences in factors such as maternal sensitivity can be explained by the stress of minority status and not due to any identifiable cultural explanations. The fact that maternal sensitivity was associated with better outcomes among minority females and majority females suggests that maternal sensitivity itself is a type of resource that is often lacking in disadvantages settings.

### *Authoritarian Versus Authoritative Parenting and Discipline*

The specific behaviors described previously are most salient at the very early, infant, stage of development. As children become slightly older, the focus shifts more to examining the impact of varying parenting and discipline strategies. Specifically, the difference between two broad categories of authoritarian and authoritative parenting has been of much interest. *Authoritarian* parenting is strict parenting demanding obedience with little input or negotiation on the side of the child (low warmth, high control) (Baumrind, 1966, 1968). *Authoritative* parenting is guided parenting allowing for the input of the child (high warmth, high control) (Baumrind, 1966, 1968). Although both types of parenting are found among all cultures, authoritarian parenting is thought to be more prevalent in Asia because of the cultural emphasis on obedience and collective harmony, whereas authoritative is more common in Europe and the Americas (Leung, Lau, & Lam, 1998; Wu et al., 2002). As useful as these categories may be, many maternal behaviors do not fit neatly along the authoritarian/authoritative spectrum. For example, a study in China showed that maternal endorsement of collectivism (as defined by the importance of the family and collective good) correlated with inductive reasoning (a characteristic of authoritative parenting) and with less adolescent aggression, whereas a high score on desiring social harmony (valuing harmonious relationships free of conflict) was linked with worse adolescent behavior, both of which are cultural values in China (Shuster, Li, & Shi, 2012). It also cannot be assumed that child phenotype, or behavioral problems, is a result of parenting because it is possible that specific child temperaments induce less warmth and more efforts at control from parenting, thus inducing an association between a specific parenting style and a child outcome (Muhtadie, Zhou, Eisenberg, & Wang, 2013). Furthermore, the consequences of each parenting style can also shift over time as the nature of the social and economic environment changes (Super & Harkness, 2002). The developmental perspective reminds us that the ultimate goal of parenting is to produce an offspring who will be most adapted to the future environment, using the resources available to the parents.

Much of the research on authoritarian parenting overlaps with that on harsh parenting. Harsh parenting includes a strong emphasis on discipline and is defined as overbearing and generally negative parenting characterized by acts of aggression such as yelling, threatening, and actual physical violence (Patterson, 1982). Although harsh parenting might be expected to be associated with increases in responsivity to the environment and a heightened HPA axis response, it is clear that children react in two distinct ways characterized as the hawk versus dove response (Korte, Koolhaas, Wingfield, & McEwen, 2005). Given similar exposures to harsh parenting, the hawk children were more likely to exhibit diminished HPA activity with an increase in sympathetic nervous system activity, whereas the dove children exhibited the opposite patterns (Sturge-Apple, Davies, Martin, Cicchetti, & Hentges, 2012). Harsh parenting is often accompanied by unpredictable parenting, which might have an independent developmental impact (Frankenhuis et al., 2013).

Although it may be tempting to assume that the negative outcomes associated with harsh and unpredictable parenting are due to the parenting, it must be considered that the parenting is in itself a response to a harsh environment. Harsh parenting itself is much more prevalent among families and communities that are marginalized across diverse cultures (Jocson, Alampay, & Lansford, 2012). This brings the suggestion that some of the cross-cultural variation may actually be variation in the harshness of the environment. Harsher parenting techniques might be a natural response to living in a harsh environment.

### *Emotional Regulation of Children*

One of the key "lessons" that is communicated to children through the various parenting approaches is the appropriateness, expression, and controllability of positive and negative emotions. Cross-cultural differences in emotional regulation have been documented with children as young as age 6 months. For example, a study by Morelen, Zeman, Perry-Parrish, and Anderson (2012) examined varying levels of emotion regulation (sadness and anger) among children (ages 8–15 years) from Ghana, Kenya, and the United States. They found that, overall, Ghanian youth were most emotionally expressive and that American children were most likely to inhibit and try to control the expression of sadness. This study is also notable for the fact that it is one of the few studies that compared the experiences of children in different areas of Africa, revealing significant heterogeneity. Comparisons of children in India and the United States have focused on differences in the expression of anger, sadness, and physical pain (Raval & Martini, 2009; Raval, Martini, & Raval, 2007). Indian children internalized that the expression of sadness or anger was less acceptable than that of physical pain. In contrast, American children were much more likely to vocalize emotions. Whereas the Indian children reported that they feared what others would think of them if they expressed anger or sadness, American children reported that they wanted to communicate what they were experiencing as a reason for doing so (Wilson, Raval, Salvina, Raval, & Panchal, 2012). Indeed, a focus in the United States on "emotional intelligence" emphasizes the naming and communication of emotions as a strategy toward emotional regulation, whereas in India, children are taught to first think about the impact on others that their anger or sadness might have (Markus & Kitayama, 1991; Raimundo, Marques-Pinto, & Lima, 2013; Zeidner, Matthews, Roberts, & MacCann, 2003).

### *Research and Ethical Implications*

The understanding that specific parenting behaviors, even if they are correlated with higher risk of mental health problems later in life, are meant to be adaptive in the current environment raises several important research and ethical implications. For example, harsh parenting may be adaptive in raising a hyperaroused and hypervigilant child, given the presence of a harsh and dangerous environment. An external intervention aimed at reducing and "calming" HPA axis activation (because it is associated with higher risk of mental health problems later in life) may induce a mismatch. In the absence of improving the external environment, the developing child may not be properly prepared to successfully negotiate it and protect him- or herself from its dangers. For example, a less aggressive youth may be at higher risk of disrespect or attack by members of his or her social group (Frankenhuis & Del Giudice, 2012).

On the other hand, an external intervention is unlikely to undo years of a specific parenting strategy, but it may provide a data point as the developing child is sampling the environment for cues as to his or her future. It can be argued that adding a highly nurturing experience may (1) promote developmental plasticity because the environmental cues are now less consistent and (2) provide skills that will be adaptive if the environment does improve (Frankenhuis & Del Giudice, 2012). This dilemma reinforces that sampling of the environment is probabilistic and sometimes it is wrong and that there is much to learn about the most important processes before we can create interventions that we can be confident will be successful.

## Combining Genes, Parenting, Culture, and Future Risk

It is not a new observation that culture shapes parenting, which in turn shapes development. The contribution of cultural neuroscience is the ability to empirically link cultural norms and behavioral expectations to their neural underpinnings. One concrete pathway toward this end is the focus on specific parenting behaviors, variation in genotype, and outcomes of interest.

### *Serotonin*

The *5-HTTLPR* genotype is an obvious candidate because of its central role in the sensitivity to the environment theories and cultural neuroscience (Caspi et al., 2010; Chiao & Blizinsky, 2010; Ellis et al., 2011). There is growing evidence that carriers of the ss versus ll alleles are differentially susceptible to the effects of caregiving (Taylor et al., 2006), although findings are not always consistent (Belsky & Pluess, 2013). For example, Hanlin et al. (2011) examined whether the correlation between parenting variables such as parental warmth and "positive parenting" and child-reported positive affect (ages 9–15 years) was different between ll, ls, and ss carriers. They found that the ss carriers had the most positive affect in the presence of warm and supportive parenting and the lowest levels of positive affect when the parenting was not warm or positive. The parenting variables studied have been very diverse and include being overly protective (Burkhouse, Gibb, Coles, Knopik, & McGeary, 2011), as well as "warm" and "positive" parenting, both observed and recollected by older children. Only a few studies have examined the potential role of the *5-HTTPLR* genotype on parenting. Pener-Tessler et al. (2013) found that among boys, carrying the s allele was associated with more self-control, which was in turn associated with more positive parenting. On the other hand, mothers who were carriers of the s allele exhibited less positive parenting toward their boys in general, and especially if they were low in self-control. No effects were found among daughters (Pener-Tessler et al., 2013). Similarly, a study of maternal sensitivity revealed that mothers carrying both ss alleles were less responsive to their toddlers than women carrying at least one l allele (Bakermans-Kranenburg & van Ijzendoorn, 2008). These findings are somewhat surprising given the hypothesis that the ss genotype increases sensitivity to the environment, which in the case of parenting might be expected to translate to high maternal sensitivity and responsiveness to her child.

### *Oxytocin*

Research on the oxytocin receptor gene (*OXTR*) began after several studies showed that the intranasal administration of oxytocin increased people's trust and altruism (Caspi et al., 2010; De Dreu et al., 2010). At the population level, variation in the oxytocin receptor gene (*OXTR* G and A alleles) has been linked with socioculturally salient traits such as empathy, trust, and sensing of others' emotions (Krueger et al., 2012; Rodrigues, Saslow, Garcia, John, & Keltner, 2009; Saphire-Bernstein, Way, Kim, Sherman, & Taylor, 2011). Those carrying the G allele tend to have more positive mental health outcomes such as greater optimism and other psychological resources (Saphire-Bernstein et al., 2011), although again, the research is far from equivocal (Cornelis et al., 2012). Similar to initial research on the *5-HTTPLR* gene that considered it a vulnerability gene only to determine that it is much more complicated, most recent research on oxytocin is also revealing a much more complex picture (Bradley et al., 2011; Lucas-Thompson & Holman, 2013). However, research is also emerging showing the detrimental side of being a trusting person: Several studies have found that carrying the G allele increased the risk associated with early childhood maltreatment, presumably because of the higher negative impact of the loss of trust and ensuring disorganized attachment (Bradley et al., 2011; McQuaid, McInnis, Stead, Matheson, & Anisman, 2013). There is also preliminary evidence that among children, one of the oxytocin receptor genes (*OXTR rs237885* and *OXTR rs2268493* A alleles) may be correlated with higher scores on the callous-unemotional scale (Beitchman et al., 2012).

Little is known about geographic differences in G and A allele frequencies and whether such frequencies would be correlated with overall cultural values of trust and empathy. A few studies have noted cross-cultural differences in the phenotypic correlates of the gene. In one study of American and Korean adults, Americans in high-stress settings (in which seeking emotional support is normative) with at least one G allele of the *OXTR* gene were more likely to seek support than Americans with the AA allele. However, this genotype effect was not observed among Koreans, for whom emotional support seeking is not normative. This was interpreted to support the idea that the G allele sensitizes one to the environment and makes one seek support when appropriate. Among the Korean participants, it was not appropriate, so there is not the same increase in emotional support seeking with the G allele (Kim et al., 2010). There is also emerging evidence that variation in the *OXTR* gene predicts parenting behaviors such as vocalizing to infant and also instrumental care (Del Giudice et al., 2011; Mileva-Seitz et al., 2013).

### *Dopamine*

The dopamine receptor genes (e.g., *DRD1, DRD2*, and *DRD4*) are involved in the brain reward system and have been associated with differences in psychological characteristics such as executive function, focus/attention, and novelty seeking (Cook et al., 1995; Reiner & Spangler, 2011; Wise & Rompre, 1989). There is evidence that the presentation of such traits may be modified by parenting (Belsky & Pluess, 2013). In a study of early childhood temperament, children with the *DRD4* 7-repeat allele were more likely to be impulsive, but only in the presence of observed lower-quality parenting (Sheese, Voelker, Rothbart, & Posner, 2007). Similar results have been found with older kids and externalizing problems (Sheese et al., 2007). Although these study designs were not able to rule out the possibility that higher impulsivity/

externalizing problems in the children had a detrimental effect on parenting, it is clear that there is an interaction between the dopamine receptor gene, child temperament, and parenting behavior. Variation in the dopamine receptors *DRD1* and *DRD2* has been found to be associated with certain specific parenting behaviors of infants, such as "orienting away" and infant-directed vocalizing (Mileva-Seitz et al., 2012). Although it remains unknown how these behaviors are modified by culture, there is evidence that haplotype frequencies of the *DRD2* receptor gene differ globally, with highest heterozygosity in Africa and lowest in East Asia as well as North and South America (Kidd et al., 1998).

## Future Directions

Not surprisingly, the research findings presented in this chapter raise more questions for cultural neuroscience than they answer. Basic questions about how and whether geographic variation in frequencies of gene haplotypes related to specific serotonin, oxytocin, or dopamine processes covary with parenting practices and norms remain unanswered. For example, given evidence that the proportion of ss allele carriers of the *5-HTTPR* genotype is correlated with aggregate collectivism, it is possible that the transmission of collectivism is partly mediated through specific parenting behaviors by ss allele-carrying parents and increased sensitivity to these inputs by their ss allele-carrying children. The absolute level of investment in children through caregiving may also be influenced by the presence of sensitivity genes. From an evolutionary perspective, high-quality parenting (however defined) takes up much energy. In a context in which most children do not carry the sensitivity allele (e.g., they are ll allele carriers), it might not be "worth it" to expend so much energy if the children are not responsive to differences in parenting (within the normal range). This hypothesis might be empirically supported by evidence from low-risk families that parenting itself is more intensive among, for example, ss allele-carrying mother–child dyads in comparison to ll allele-carrying mother–child dyads.

These interactions between culture, parenting, genotype, and mental health risk are likely much more complicated than we currently imagine. An emerging theme is that the sheer harshness of an impoverished environment likely modifies whether a given phenotype is associated with resilience or vulnerability. Whereas a sensitive genotype might be associated with specific normative cultural values (e.g., collectivism), a more insensitive genotype might be associated with resilience to the harsh environment (Mesman et al., 2012)—empirical evidence is needed to examine this idea further. It is imperative for health disparities researchers to better understand what ultimately determines risk or resilience.

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