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Enhancing visual perceptual learning using transcranial electrical stimulation: Transcranial alternating current stimulation outperforms both transcranial direct current and random noise stimulation

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Diverse strategies can be employed to enhance visual skills, including visual perceptual learning (VPL) and transcranial electrical stimulation (tES). Combining VPL and tES is a popular method that holds promise for producing significant improvements in visual acuity within a short time frame. However, there is still a lack of comprehensive evaluation regarding the effects of combining different types of tES and VPL on enhancing visual function, especially with a larger sample size. In the present study, we recruited four groups of subjects (26 subjects each) to learn an orientation discrimination task with five daily training sessions. During training, the occipital region of each subject was stimulated by one type of tES—anodal transcranial direct current stimulation (tDCS), alternating current stimulation (tACS) at 10 Hz, high-frequency random noise stimulation (tRNS), and sham tACS—while the subject performed the training task. We found that, compared with the sham stimulation, both the high-frequency tRNS and the 10-Hz tACS facilitated VPL efficiently in

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terms of learning rate and performance improvement, but there was little modulatory effect in the anodal tDCS condition. Remarkably, the 10-Hz tACS condition exhibited superior modulatory effects compared with the tRNS condition, demonstrating the strongest modulation among the most commonly used tES types for further enhancing vision when combined with VPL. Our results suggest that alpha oscillations play a vital role in VPL. Our study provides a practical guide for vision rehabilitation.

Introduction

Our visual system is remarkably malleable (i.e., has visual plasticity) throughout the entire life span, for both mature and degenerative brains. It has been well documented that various methods can bring about visual plasticity, such as extensive training and non-invasive brain stimulation techniques (He, Yang, Zhao, & Fang, 2022). Regarding visual plasticity induced by extensive training (i.e., visual perceptual learning [VPL]), many advancements have been made in unveiling its characteristics, brain loci, and neural manifestations over the last three decades (He, Yang, & Zhao, 2022). More importantly, VPL has been widely applied in various fields (Lu, Lin, & Dosher, 2016), such as low-vision rehabilitation (Huang et al., 2022; Levi & Polat, 1996), remediation for dyslexia (Gori & Facoetti, 2014; Meng, Lin, Wang, Jiang, & Song, 2014), x-ray security screening (McCarley, Kramer, Wickens, Vidoni, & Boot, 2004), sports and military training (Hadlow, Panchuk, Mann, Portus, & Abernethy, 2018), and medical imaging education (Alexander, Waite, Macknik, & Martinez-Conde, 2020). At the same time, our visual plasticity can also be induced by transcranial electrical stimulation (tES)—a non-invasive neuromodulatory technique in which weak electrical fields are delivered through electrodes positioned on the scalp surface. The three most common types of tES techniques are categorized based on the current waveform: transcranial direct current stimulation (tDCS) (Nitsche & Paulus, 2000; Priori, Berardelli, Rona, Accornero, & Manfredi, 1998), transcranial alternating current stimulation (tACS) (Antal et al., 2008), and transcranial random noise stimulation (tRNS) (Terney, Chaieb, Moliadze, Antal, & Paulus, 2008). All of these three types of tES techniques have been found to be able to modify cortical excitability and modulate visual functions in both healthy and clinical populations (Bello et al., 2023), such as contrast sensitivity (Antal, Nitsche, & Paulus, 2001; Potok et al., 2023), visual acuity (Bocci et al., 2018; Reinhart, Xiao, McClenahan, & Woodman, 2016), motion direction discrimination (Battaglini et al., 2023; Ghin, Pavan, Contillo, & Mather, 2018), and peripheral target identification in a crowded environment (Battaglini, Ghiani, Casco, & Ronconi, 2020; Chen, Zhu, He, & Fang, 2021), thus establishing causal links between brain activity and cognitive functions (Zhang, Zhang, Cai, Luo, & Fang, 2019).

Currently, there is an increasing focus on modulating VPL by tES, which is both theoretically significant and practically useful. Theoretically, through selective modulation of the brain during distinct phases of learning, mechanisms that support successful task acquisition and consolidation may be more fully characterized (He, Yang, & Fang, 2021; He, Yang, Gong, Bi, & Fang, 2022; He, Yang, & Zhao, 2022; Wu et al., 2023; Yang, He, & Fang, 2022). From the perspective of translational applications, attaining the greatest training benefits effect in the briefest time frame provides most benefit to subjects, whereas in a typical practical-oriented application case thousands of trials across multiple training sessions are usually required. Therefore, boosting VPL by tES is expected to accelerate learning and allow subjects to obtain greater benefits (He, Yang, & Gong, 2022; Herpich et al., 2019).

Different types of tES have been adopted to modulate VPL (for a review, see He, Yang, & Zhao, 2022). With regard to the effect of tDCS on modulating VPL, the results are mixed, and no consistent result has been found regardless of whether tDCS was administered before task execution (offline mode) or during task execution (online mode). For example, when tDCS was applied during task execution, anodal tDCS was found to be effective in boosting VPL in some studies (Frangou, Correia, & Kourtzi, 2018; Wu et al., 2023), but in other studies no obvious modulatory effect was found (Fertonani, Pirulli, & Miniussi, 2011; Herpich et al., 2019; Larcombe, Kennard, O'Shea, & Bridge, 2018; Larcombe et al., 2018; Wu et al., 2022), and even a suppressive effect was observed (Jia et al., 2022b). Studies using offline tDCS in VPL tasks showed similarly conflicting results (Pirulli, Fertonani, & Miniussi, 2013; Pirulli, Fertonani, & Miniussi, 2014; Wu et al., 2023). By contrast, the results of modulating VPL by tRNS are relatively consistent. Specifically, high-frequency (100–640 Hz) tRNS boosts VPL effectively in both healthy and clinical populations (Camilleri, Pavan, Ghin, Battaglini, & Campana, 2014; Campana, Camilleri, Pavan, Veronese, & Lo Giudice, 2014; Cappelletti, Pikkat, Upstill, Speekenbrink, & Walsh, 2015; Conto et al., 2021; Donkor et al., 2021). With regard to tACS, although the underlying neural mechanisms of action of tACS on the brain are relatively clear among tES techniques (Johnson et al., 2020; Krause, Vieira, Csorba, Pilly, & Pack, 2019; Zaehle, Rach, & Herrmann, 2010), only limited studies have been conducted to modulate VPL. Specifically, when we previously stimulated subjects' visual cortical areas with tACS at different frequencies, we found that only occipital 10-Hz tACS was able to boost VPL, and no such effect was found for other stimulation frequencies (e.g., 6, 20, and 40 Hz) (He, Yang, & Gong, 2022). Similarly, in another study, occipital 3-Hz tACS was found to show little effect on VPL (Zizlsperger, Kummel, & Haarmeier, 2016). Moreover, we also found that the modulatory effect of 10-Hz tACS was absent when other cortical areas were stimulated (He, Yang, & Gong, 2022). Altogether, these studies demonstrate that tACS facilitates VPL in a frequency- and location-specific manner.

Despite advancements in VPL being observed following the application of diverse types of tES, a systematic evaluation of the modulatory effects of tES on VPL is still lacking. Notably, studies on modulating VPL by tES usually employ a relatively small sample size design, raising the risk of sampling bias and limiting the generalizability of those findings (Minarik et al., 2016). We recruited four groups of subjects to learn an orientation discrimination task, and each group received a specific form of stimulation, including sham, tDCS, high-frequency tRNS, and 10-Hz tACS during their training phase. Notably, there were 26 participants in each group, which provided sufficient statistical power and representativeness to ensure the reliability and generalizability of our findings.

Methods

Subjects

A total of 104 right-handed healthy adults with normal or correct-to-normal vision took part in the present study. Subjects were assigned to one of four conditions (26 subjects in each condition): anodal tDCS (11 females; mean age, 21.54 ± 2.42 years), high-frequency tRNS (20 females; mean age, 21.77 ± 2.21 years), 10-Hz tACS (18 females; mean age, 21.15 ± 4.58 years), and sham 10-Hz tACS (17 females; mean age, 22.04 ± 2.89 years). The sample sizes were determined based on our previous study (alpha level = 0.05, power = 80%, two-tailed Cohen's $d = 0.96$) (He, Yang, & Gong, 2022). Specifically, all data from that study (He, Yang, & Gong, 2022) for the 10-Hz tACS condition ($n = 21$) and the sham 10-Hz tACS condition ($n = 20$) were included in the present study, and all other data were newly collected. We recruited five more subjects for the 10-Hz tACS condition and six more subjects for the sham stimulation condition in the present study to obtain more robust results. A screening questionnaire was administrated for each subject before starting the study. Subjects were excluded if they met the following criteria: (1) age older than 30 years or younger than 18 years, (2) a history of neural surgery or epileptic seizures or any psychiatric or neurological disorders, (3) sleep disorders or a total sleep time less than 7 hours per night over the last 2 weeks, or (4) during the ovulation phase of the menstrual cycle or pregnancy (He et al., 2019; He, Yang, & Gong, 2022). All experimental protocols and procedures were approved by the Ethics Committee of the School of Psychological and Cognitive Sciences at Peking University. Before participation, informed written consent was obtained from each subject.

Apparatus and stimulation protocol

MATLAB R2015a (MathWorks, Natick, MA) and Psychtoolbox-3 extensions (Brainard, 1997) were used to generate and control visual stimuli, which were presented on a liquid crystal display (LCD) monitor (Display++ LCD Monitor; Cambridge Research Systems, Rochester, UK) with a gray background (mean luminance = 30 cd/m^2, width = 70 cm, spatial resolution = 1920 × 1080 pixels, refresh rate = 120 Hz). The only source of light in the room was the monitor. The head of each subject was fixed on a chin and head rest at a viewing distance of 70 cm. To ensure that the subject's eye position was stable within 1° from the fixation point when visual stimuli were presented, the EyeLink 1000 Plus eye-tracking system (SR Research Ltd., Ottawa, ON, Canada) was used to monitor subjects' eye movements throughout the entire experiment.

The high-frequency (100–640 Hz) tRNS was delivered by a battery-powered current stimulator (DC-Stimulator Plus; neuroConn GmbH, Ilmenau, Germany), and the current in other forms was delivered using the DC-Stimulator MC (neuroConn) through a pair of rubber electrodes that were 5 × 7 cm^2. The electrodes were inserted into two soaked sponges (0.9% saline solution) and attached to the scalp of each subject by two elastic bandages. The current intensity was a constant 2.0 mA for anodal tDCS, and the peak-to-peak current intensity was 2.0 mA for tACS and high-frequency tRNS. The current in both active and sham tACS stimulation conditions was in the form of a sine wave. The phase difference between the two stimulation electrodes was set at zero. In each session of all stimulation conditions, the impedance was kept lower than 6 KΩ.

Visual stimuli and task

The task paradigm and the stimulus setup used in this study were the same as in our previous studies (He et al., 2021; He, Yang, & Gong, 2022). Oriented Gabor patches with noise (diameter = 1.25°; spatial frequency = 3.0 c/°; Michelson contrast = 0.5; standard deviation of Gaussian envelope = 0.42°; random spatial phase; 25%

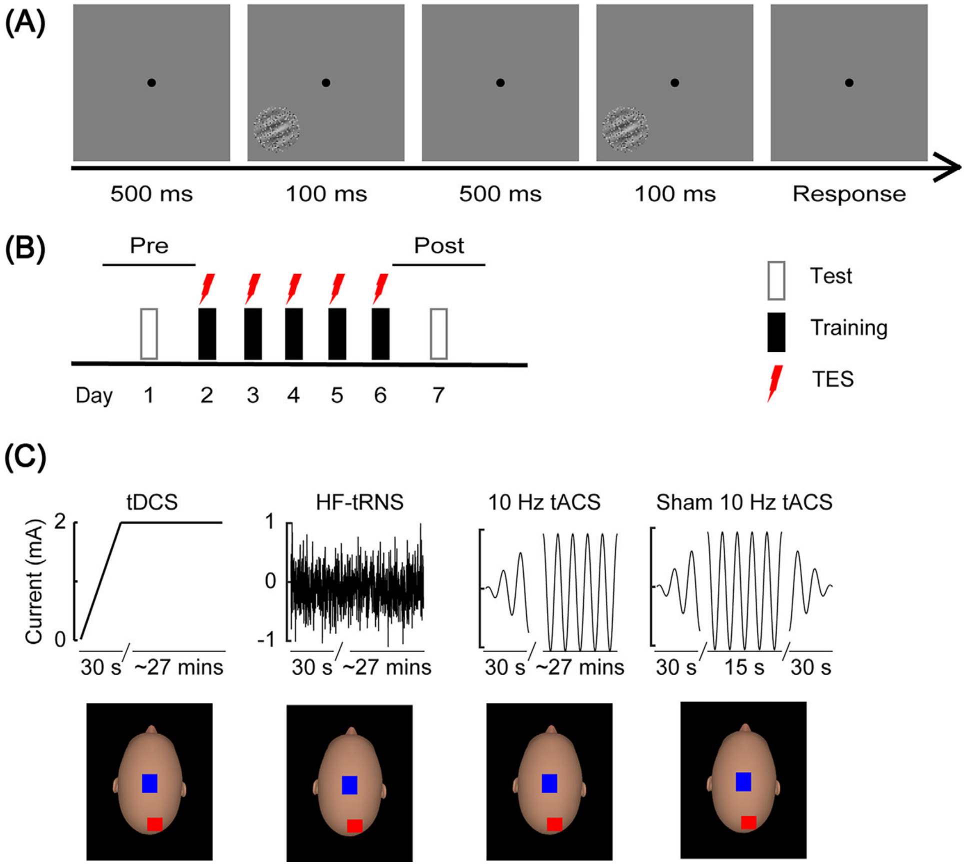

Figure 1. Stimuli, experimental design, and electrical stimulation protocol. (**A**) Schematic description of a 2AFC trial in a QUEST staircase for measuring orientation discrimination thresholds. Subjects were instructed to make a judgment of the orientation in the second interval relative to that in the first interval (clockwise or counterclockwise) while gazing at the central fixation point. No feedback was provided after each trial. (**B**) Experimental protocol. Subjects underwent a pretraining test, five daily training sessions, and a post-training test. The pretraining test (Pre) and post-training test (Post) took place on the days before and immediately after training, respectively. The tES was concurrently administrated during each training session. (**C**) Electrical stimulation protocol and montage. tES with different current waveforms (tDCS, tRNS, and tACS) was applied concurrently during each training session. Stimulation electrodes were positioned over the occipital cortex (O2) and the vertex (Cz). The electrode positions were defined by the international 10–20 EEG system. The red square and blue square denote the anodal electrode and cathodal electrode, respectively. These head models were generated by FaceGen Modeller 3.4.

of the pixels in these patches were replaced with random noise) were presented in the lower left quadrant of the visual field, 5° from the fixation point. In each trial, a small fixation point was presented first for 500 ms, followed by two Gabor patches with orientations of 26° and $26° + \theta$, which appeared 100 ms each in a random order with a 500-ms blank interval (Figure 1A). A two-alternative forced-choice (2AFC) method was used in the task, and subjects were instructed to judge the orientation change of the second Gabor patch relative to the first one (counterclockwise or clockwise) by pressing keys. Subjects' orientation discrimination thresholds at 75% accuracy were estimated using a QUEST staircase procedure, such that the θ varied trial by trial (Watson & Pelli, 1983). Subjects rested after each staircase. No feedback was provided in all test and training sessions.

Design

A single-blind, sham-controlled, between-subjects design was adopted to explore the modulatory effect of different types of tES on orientation discrimination learning. Subjects were trained on the orientation discrimination task for five consecutive days. Before and after the five daily training sessions, test sessions were conducted: pretraining (Pre) and post-training (Post) (Figure 1B). Each test session and each training session consisted of six and nine QUEST staircases of 50 trials, respectively.

The hemisphere contralateral to the visual field where the visual stimuli were presented was stimulated. Two electrodes were placed over each subject's visual cortex and vertex (i.e., O2 and Cz in the international 10–20 EEG system, respectively) (Figure 1C). Electrical stimulation was delivered concurrently with training, with a ramp-up of 30 seconds at the beginning of each training session.

Statistical analysis

The threshold for each session was estimated by calculating the geometric mean of thresholds from all QUEST staircases in that session. The performance change after training was quantified by calculating the percent improvement as [(*pretraining threshold – post-training threshold*)/*pretraining threshold*] × 100%. All estimated thresholds were then normalized: The estimated threshold for each session was divided by the estimated threshold at Pre and then multiplied by 100%. In order to describe the process of threshold change during the learning course, we fitted the learning curves of normalized orientation discrimination thresholds across all sessions using a power function:

$$\log_{10}(Th(t)) = \rho \times \log_{10}(t)$$

In this function, *Th* represents the predicted normalized threshold, *t* is the number of training sessions, and ρ is the learning rate (Yang et al., 2020). The threshold declines with training, such that the value of ρ should be negative, and a smaller value indicates a faster learning speed. To minimize the sum of squared differences between model predictions and observed values, a nonlinear, least-square method was implemented in MATLAB.

A mixed-design analysis of variance (ANOVA) using *Condition* as a between-subjects factor (tDCS, tRNS, tACS, and sham) was used to analyze the orientation discrimination thresholds. Raw thresholds at Pre, learning rates, and percent improvements were analyzed by ANOVA using *Condition* as a between-subjects factor. We used the Benjamini–Hochberg method to control the false discovery rate for multiple comparisons. Partial eta squared (η_p^2) and Cohen's *d* were calculated to measure the effect size for ANOVAs and *t*-tests. Statistical analyses were conducted using R (R Foundation for Statistical Computing, Vienna, Austria) (R Core Team, 2023).

Results

Training improved task performance substantially

First, a one-way ANOVA with *Condition* (tDCS, tRNS, tACS, and sham) as a between-subjects factor on the thresholds at Pre was conducted to examine the baseline variance among all enrolled conditions. The statistical results showed that the main effect of *Condition* was not significant, $F(3, 100) = 0.37$, $p = 0.79$, $\eta_p^2 = 0.01$, demonstrating that subjects had comparable baseline performance across all stimulation conditions (Figure 2A). Next, to assess the learning effect on the trained task, we employed a mixed-design ANOVA that incorporated *Session* (Pre and Post) as a within-subjects factor, *Condition* as a between-subjects factor, and the subjects' orientation discrimination thresholds as the dependent variable. The statistical results showed that the main effect of *Session*, $F(1, 100) = 207.89$, $p < 0.001$, $\eta_p^2 = 0.68$, and the interaction between *Session* and *Condition*, $F(3, 100) = 3.29$, $p = 0.02$, $\eta_p^2 = 0.09$, were significant, but the main effect of *Condition*, $F(3, 100) = 0.95$, $p = 0.42$, was not significant, demonstrating that the subjects' performance improved after training and the performance improvement was different across all stimulation conditions. Further analyses showed that the thresholds at Post were lower than those at Pre for all stimulation conditions: for sham, $t(25) = 4.33$, $p_{adj} < 0.001$, Cohen's $d = 0.85$; for tDCS, $t(25) = 6.77$, $p_{adj} < 0.001$, Cohen's $d = 1.33$; for tRNS, $t(25) = 10.21$, $p_{adj} < 0.001$, Cohen's $d = 2.00$; for tACS, $t(25) = 9.01$, $p_{adj} < 0.001$, Cohen's $d = 1.77$ (Figure 2B). Importantly, no feedback was provided during the training course, suggesting that subjects acquired the improved ability to discriminate the trained stimuli in an unsupervised learning manner (Frank et al., 2020; Tsodyks & Gilbert, 2004).

Learning rate was modulated by tES

The efficiency of performance improvement in learning is typically quantified by learning rate, which in this case is represented by the ρ value. We examined ρ-value differences among the different stimulation conditions. A one-way ANOVA revealed that the main effect of *Condition* on ρ value was significant, $F(3, 100) = 9.20$, $p < 0.001$, $\eta_p^2 = 0.22$, demonstrating that subjects in different stimulation conditions showed different learning rates (Figure 2C). Specifically, pairwise *t*-tests showed that there was no significant difference between the sham condition and the tDCS condition in learning rate, $t(50) = 0.90$, $p_{adj} = 0.38$, Cohen's $d = 0.25$, whereas the learning rates in both the tRNS and the tACS conditions were significantly greater than that in the sham condition: for tRNS versus sham, $t(50) = 2.90$, $p_{adj} = 0.01$, Cohen's $d = 0.80$; for tACS versus sham, $t(50) = 4.44$, $p_{adj} < 0.001$, Cohen's $d = 1.23$. Compared with the tDCS condition, the learning rate in the tACS condition was higher, $t(50) = 3.76$, $p_{adj} = 0.001$, Cohen's $d = 1.04$, but no such effect was found in the tRNS condition, $t(50) = 2.03$, $p_{adj} = 0.06$, Cohen's $d = 0.56$. Moreover, the learning

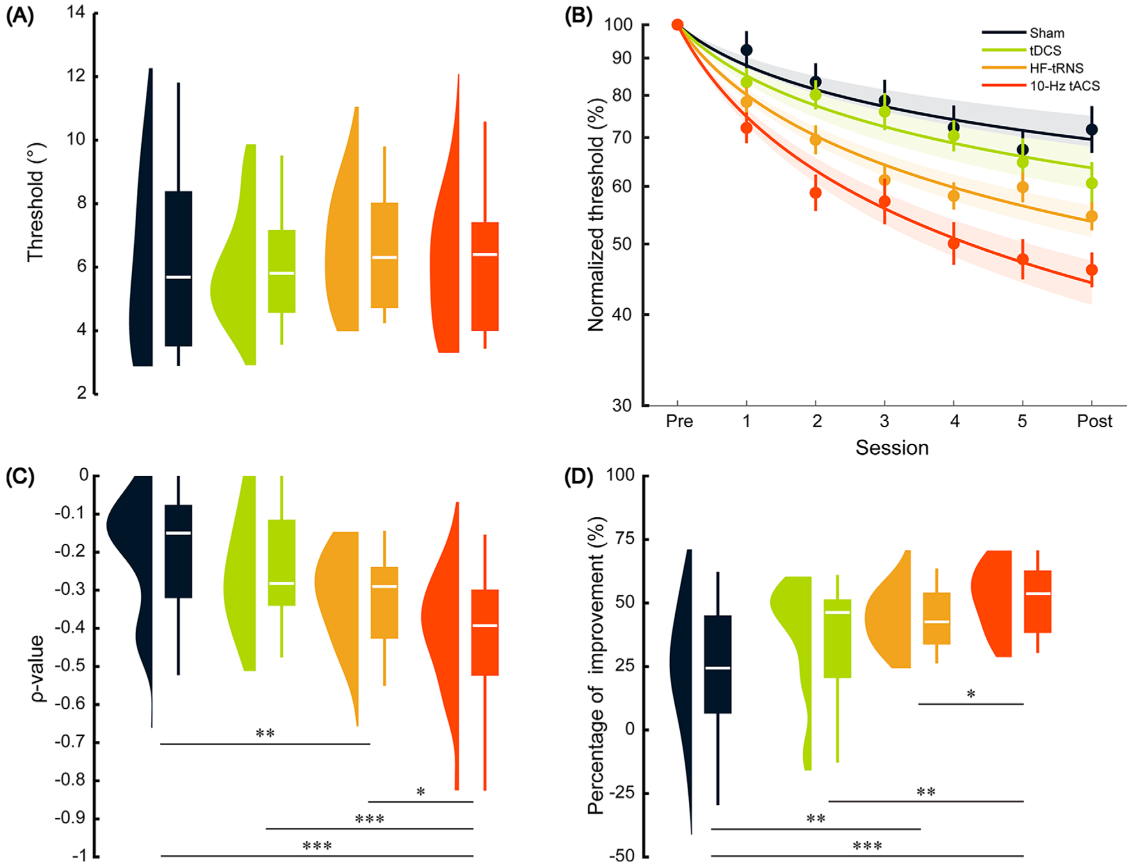

Figure 2. Main results. (**A**) Thresholds at Pre. (**B**) Normalized learning curves. Dots represent averaged thresholds across subjects at different test and training sessions, and lines represent fitted learning curves using a power function. Note that the *y*-axis is displayed on a logarithmic scale. (**C**) Learning rate for each condition; a smaller value indicates a faster learning speed. (**D**) Percentage of improvement in orientation discrimination performance. $^{*}p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$. Error bars denote 1 *SEM* across subjects.

rate in the tACS condition was higher than that in the tRNS condition, $t(50) = 2.27$, $p_{\text{adj}} = 0.04$, Cohen's $d =$ 0.63. In short, the application of 10-Hz tACS during training yielded the most rapid acceleration of the orientation discrimination learning.

Performance improvement was modulated by tES

The space for improvement in learning is of great concern to both basic and clinical researchers. Here, we examined percent improvement differences among the different stimulation conditions. Percent improvement among the stimulation conditions was significant, as revealed by a one-way ANOVA, $F(3, 100) = 9.69$, $p <$ 0.001, $\eta_p^2 = 0.23$ (Figure 2D). Further analyses showed that the percent improvement in the 10-Hz tACS condition was significantly higher than those in all other stimulation conditions: for tACS versus sham, $t(50) =$ 4.85, $p_{\text{adj}} < 0.001$, Cohen's $d = 1.35$; for tACS versus tDCS, $t(50) = 3.08$, $p_{\text{adj}} = 0.008$, Cohen's $d = 0.85$; for tACS versus tRNS, $t(50) = 2.33$, $p_{\text{adj}} = 0.04$, Cohen's d $= 0.65$. Notably, the performance improvement in the tRNS condition was significantly higher than that in the sham condition, $t(50) = 3.55$, $p_{\text{adj}} = 0.003$, Cohen's $d = 0.98$. All other differences among the stimulation conditions were not significant: for tDCS versus sham, $t(50) = 1.74$, $p_{\text{adj}} = 0.11$, Cohen's $d = 0.48$; for tDCS versus tRNS, $t(50) = 1.60$, $p_{\text{adj}} = 0.12$, Cohen's $d =$ 0.44. In short, after training with concurrent occipital 10-Hz tACS, subjects exhibited the most pronounced improvement in their performance on the trained orientation discrimination task.

In summary, subjects' task performance improved with training from comparable initial performance levels. The modulatory effects of tES on VPL were strongly dependent on the stimulation type. Specifically, anodal tDCS applied during execution of the orientation discrimination task had little effect on modulating the acquisition of learning to discriminate the stimuli. By contrast, both high-frequency tRNS and 10-Hz tACS were capable of facilitating orientation discrimination learning, in terms of both learning rate and overall performance improvement achieved. Finally, occipital 10-Hz tACS showed the best modulatory effects.

Discussion

In the present study, we evaluated the effect of several of the most common types of tES techniques (i.e., tDCS, tRNS, and 10-Hz tACS) on the further enhancement of vision by modulating VPL. Our results revealed distinct modulatory effects of tES with different current forms when applied during learning on the orientation discrimination task. Specifically, compared with the sham stimulation, anodal tDCS showed little effect on modulating VPL, but both high-frequency tRNS and 10-Hz tACS were effective in boosting VPL. Additionally, 10-Hz tACS exhibited a superior modulatory effect compared to the other current stimulation forms. To the best of our knowledge, the current study is the first to systematically evaluate the effects of various types of tES techniques on modulating VPL. Importantly, compared with previous studies investigating the modulatory effects of tES on VPL, the present study has the largest sample size (~30 subjects per condition), thus ensuring sufficient statistical power for between-condition comparisons. In short, our findings will provide guidance for translational applications of combining VPL and tES, as well as insights into the neural mechanisms of VPL.

We found that anodal tDCS applied concurrently with training had no effect on modulating VPL, which is consistent with previous studies in short-term orientation discrimination learning (Fertonani et al., 2011) or in multi-session learning on motion direction discrimination (Fertonani, Pirulli, Bollini, Miniussi, & Bortoletto, 2019; Herpich et al., 2019; Larcombe & Kennard, 2018; Larcombe & Kulyomina, 2018; Wu et al., 2022). However, our results are not consistent with some studies in which anodal tDCS was effective in facilitating VPL (Olma et al., 2013; Sczesny-Kaiser et al., 2016; Van Meel, Daniels, de Beeck, & Baeck, 2016; Wu et al., 2023), or even impairing VPL with a short training session (Grasso, Tonolli, Bortoletto, & Miniussi, 2021; Grasso, Tonolli, & Miniussi, 2020; Jia et al., 2022a; Learmonth, Thut, Benwell, & Harvey, 2015). The discrepancies among these studies mentioned above can be caused by many factors, such as training tasks, training regimes, and stimulation settings. Of note, the small sample sizes adopted in previous studies may have biased the results (Minarik et al., 2016). Here, using a relatively large sample size design, we found that applying anodal tDCS concurrently during training had a negligible effect on enhancing VPL. The null effect of anodal tDCS on modulating VPL during training might be caused by the timing of the stimulation applied. Previous studies have found that anodal tDCS applied prior to task execution (i.e., the offline mode) was effective in boosting VPL (Pirulli et al., 2013), but no such modulatory effect was found when anodal tDCS was administrated during performance of the orientation discrimination task (i.e., the online mode) (Pirulli et al., 2013), just like the findings in the present study.

We found that high-frequency tRNS was effective in boosting VPL, which is consistent with previous studies (Camilleri et al., 2014; Camilleri, Pavan, & Campana, 2016; Contemori, Trotter, Cottereau, & Maniglia, 2019; Conto et al., 2021; Herpich et al., 2019). The consistent modulatory effects of high-frequency tRNS on VPL might be a result of strengthened attentional network. Functional connectivity within the attentional network was found to be increased after high-frequency tRNS, which was positively correlated with the magnitude of improvement in task performance (Conto et al., 2021).

We found that occipital 10-Hz tACS boosted VPL efficiently. Notably, more subjects were added in the present study, making our previous findings more robust (He, Yang, & Gong, 2022). In our previous study, we found that tACS boosts orientation discrimination learning in a frequency- and location-specific manner. Specifically, occipital 10-Hz tACS administrated during training resulted in the subjects learning to discriminate the orientations of task stimuli faster and achieving greater improvement compared with the sham 10-Hz stimulation condition. Furthermore, the modulatory effect was absent in other stimulation conditions, such as occipital tACS at other alternating frequencies (6, 20, and 40 Hz) and 10-Hz tACS over other cortical regions (He, Yang, & Gong, 2022). Additionally, in another study, researchers found that tACS at 3 Hz was not effective in modulating VPL (Zizlsperger et al., 2016). Taken together, these results demonstrate that occipital tACS modulates VPL in a frequency-specific manner, providing strong evidence for the vital role of alpha oscillations in gating VPL (Bays, Visscher, Le Dantec, & Seitz, 2015; Michael, Covarrubias, Leong, & Kourtzi, 2023).

Further, we also found that occipital 10-Hz tACS showed a stronger modulatory effect than occipital tRNS in visual perceptual learning. It should be pointed out that this study is the first investigation, to the best of our knowledge, to compare the modulatory effects of tACS and tRNS on VPL. Differences found in the modulatory effects on VPL between 10-Hz tACS and tRNS might reflect the inherent dissimilarities between these two types of tES techniques in modulating attention-related cognitive processing. It has been clearly demonstrated that 10-Hz tACS can directly entrain alpha power by aligned phase coherence or spike-timing (Huang et al., 2021; Johnson et al., 2020; Krause et al., 2019), such that attention-related cognitive processing is strengthened by occipital tACS at 10 Hz directly (Clayton, Yeung, & Cohen Kadosh, 2019). In contrast, high-frequency tRNS over the occipital regions may not modulate attentional processing efficiently. Previous studies have shown that applying high-frequency tRNS over the parietal regions can improve visual attention (Edwards, Contò, Bucci, & Battelli, 2020; Shalev, De Wandel, Dockree, Demeyere, & Chechlacz, 2018; Tyler, Conto, & Battelli, 2018), but no such effect was observed when stimulating the visual areas (Conto et al., 2021; Conto, Tyler, Paletta, & Battelli, 2023; Tyler et al., 2018). Therefore, the superior modulatory effects of occipital 10-Hz tACS on VPL compared to high-frequency tRNS may be attributed to different efficacies to mediate attentional processes. Here, this explanation is referred to as the efficacy of attention hypothesis, which requires further investigation in the future.

Our findings will provide a practical guide for vision rehabilitation. VPL has been widely adopted to restore low-vision in neuroophthalmology (Lu et al., 2016). In practice, it is a common desire of patients and their families to achieve the best effect in a short course of treatment (He, Yang, & Gong, 2022). However, typical clinic-oriented studies require weeks to months of training and consist of thousands of trials, placing a significant economic and psychological burden on both the patients' families and society in general (Herpich et al., 2019). Therefore, developing methods that can speed up the process and improve the treatment effectiveness is currently a hot research topic. Our results show that 10-Hz tACS over visual areas during training accelerated the learning process and maximized learning gains in healthy adults, findings that are expected to be significant for patients who need to learn or relearn skills due to injuries or illnesses. Overall, our findings have the potential to significantly impact the field of vision habilitation (Herpich et al., 2019; Huang et al., 2022; Wu et al., 2023), and further studies will help to fully determine the effectiveness of this method for patients. For example, researchers have found that patients with cortical blindness (vision loss caused by damage to the primary visual cortex) regained the ability to discriminate visual motion direction after extensive training concurrent with high-frequency tRNS (Herpich et al., 2019). The current study, however, has potential limitations with regard to clinical applications. For example, in this study, the majority of the participants were under the age of 30 years, and it is unclear if the protocols employed would be applicable to other populations (e.g., those of an elderly age) or other training tasks.

Keywords: transcranial electrical stimulation, tDCS, tACS, tRNS, visual perceptual learning, visual plasticity, unsupervised learning, implicit learning

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