Anodal online transcranial direct current stimulation (tDCS) facilitates visual motion perceptual learning

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Abstract

Visual perceptual learning (VPL) has great potential implications for clinical populations, but adequate improvement often takes weeks to months to obtain; therefore, practical applications of VPL are limited. Strategies that enhance visual performance acquisition make great practical sense. Transcranial direct current stimulation (tDCS) could be beneficial to VPL, but thus far, the results are inconsistent. The current study had two objectives: (1) investigate the effect of anodal tDCS on VPL and (2) determine whether the timing sequence of anodal tDCS and training influences VPL. Anodal tDCS was applied on the left human middle temporal (hMT+) during training on a coherent motion discrimination task (online), anodal tDCS was also applied before training (offline), and sham tDCS was applied during training (sham). The coherent thresholds were measured without stimulation before, 2 days after and one month after training. All participants trained for 5 consecutive days. Anodal tDCS resulted in more performance improvement when applied during daily training but not when applied before training. Additionally, neither within-session improvement nor between-session improvement differed among the online, offline and sham tDCS conditions. These findings contribute to the development of efficient stimulation protocols and a deep understanding of the mechanisms underlying the effect of tDCS on VPL.

INTRODUCTION

Visual perceptual learning (VPL) is a phenomenon in which intensive practice results in a dramatic and long-lasting improvement in visual perceptual abilities from visual feature discrimination to complex object recognition (Deveau et al., 2013; Lu et al., 2016). VPL demonstrates experience-dependent neural plasticity in the human brain, especially for adults who have experienced a critical period of perceptual development during their early lives (Bavelieret al., 2010; Kawato et al., 2014). Over the past decades, numerous studies have mainly focused on the cortical loci in which plastic changes occur and on the form in which plastic changes are manifested (He et al., 2022). Notably, VPL is translating from the laboratory to the clinic and commerce (Lu et al., 2016). It has been shown that VPL can serve as an enhancement or remediation method for visually impaired populations, such as those with cortical blindness (Herpich et al., 2019), amblyopia (Astle et al., 2011; Huang et al., 2008), macular degeneration (Astle et al., 2015), myopia (Tan & Fong, 2008; Yan et al., 2015), and presbyopia (Sterkin et al., 2018). However, the main challenge in practical applications of VPL is maximizing the training effects within a limited time, since a long duration of training is frequently required to obtain an adequate performance enhancement (Herpich et al., 2019).

Among noninvasive transcranial electrical stimulation (tES) techniques, transcranial direct current stimulation (tDCS) is particularly attractive due to its low cost and portability (Reinhart et al., 2016). tDCS transiently modulates cortical excitation and inhibition by altering the membrane potential of neurons (Stagg et al., 2011; Stagg & Nitsche, 2011). tDCS may be an effective tool to promote VPL. For example, the application of anodal tDCS over the human middle temporal (hMT+) and primary motor cortex (M1) improved performance in the early phase of visuomotor coordination learning, revealing the facilitated effect of tDCS on VPL for the first time (Antal et al., 2004a). In another study, participants learned a visual orientation-discrimination task during 20 min of tDCS. Their learning of orientation discrimination and cortical excitability were significantly improved by anodal tDCS over the primary visual cortex (V1) for four consecutive days compared to that after cathodal and sham tDCS (Sczesny-Kaiser et al., 2016). Recently, the right occipito-temporal cortex (OCT) was stimulated during training on a signal-in-noise task. The results demonstrated that anodal tDCS during training boosted learning by decreasing GABA+ and changing local processing in the visual cortex and altering functional connectivity between visual and posterior parietal areas (Karlaftis et al., 2021). These data provide evidence that visual gains caused by behavioral training are enhanced when combined with tDCS.

However, some studies have demonstrated the diverse effects of tDCS on VPL. For example, no tDCS effect on VPL was found when participants trained on a direction discrimination task (Fertonani et al., 2011; Herpich et al., 2019; Larcombe et al., 2018). Furthermore, overnight consolidation of VPL was even blocked by anodal tDCS applied during training on a contrast detection task (Peters et al., 2013). Thus, more evidence is needed to investigate the relationship between tDCS and VPL. For this reason, the main purpose of this study was to further verify the combined effect of tDCS and VPL.

Interestingly, the time sequence of stimulation and training may influence the tDCS effect on VPL. Pirulli et al. (2013) applied transcranial random noise stimulation (tRNS), anodal tDCS and sham tDCS on V1 before or during training on an orientation discrimination task. They found that anodal tDCS was applied before the training rather than during the training, resulting in a significant improvement in performance. These results suggested that the tDCS effects highly depend on the order of the stimulation and training. They explained that anodal tDCS induced depolarization that mainly relied on the initiation of homeostatic mechanisms. These homeostatic mechanisms might not be completely functional if engaged during training, but they should eventually present stronger aftereffects. Conversely, more research found that when tDCS was applied online (during training), it better facilitated VPL (Karlaftis et al., 2021; Sczesny-Kaiser et al., 2016). Thus, the second aim is that if tDCS has an effect on VPL, which of the two types of time sequences (before vs. during training) could produce the maximum effect?

Coherent motion is frequently employed to investigate the tDCS effect on visual perception (Battaglini et al., 2017; Battaglini et al., 2020; Olma et al., 2013) since it involves a specific brain region (i.e., hMT+) that serves as a stimulus target. Multiple techniques have confirmed the involvement of hMT+ in motion visual perception, such as electrophysiology (Britten et al., 1992), lesion (Newsome & Pare, 1988), brain imaging (Chen et al., 2016; Chen, et al., 2017) and stimulation. For example, our previous study showed that the offline application of 20-min anodal tDCS on the left hMT+ significantly improved motion perception (Wu et al., 2020). Additionally, Battaglini et al. (2020) found an online effect of anodal tDCS over the left hMT+ on a motion perception task. These results suggest the involvement of the left hMT+ in visual motion perception.

This study aimed to investigate the following two questions: (1) Does anodal tDCS affect VPL? (2) Does the time sequence of anodal tDCS influence VPL? Thus, anodal or sham high-definition tDCS (HD-tDCS) was applied over the left hMT+ during or before training for coherent motion direction identification. The whole VPL phase consisted of 5-day consecutive training sessions. Compared with the conventional approach with two large sponge electrodes, HD-tDCS uses small electrodes and has been confirmed to have the advantage of taking more focal current on the target brain regions (Dmochowski et al., 2011).

MATERIALS AND METHODS

Participants

Thirty-six participants with normal or corrected-to-normal visual acuity (VA; mean age 20.69 $\pm$ 0.9 years; 13 females) were randomly assigned to receive online ($n = 12$), offline ($n = 12$) and sham ($n = 12$) tDCS. There was no significant difference among these three conditions regarding age ($p = 0.206$), VA ($p = 0.577$) and sex ($p = 0.887$). None of the participants had previously participated in visual perception experiments and were naïve to the objective of the study. They provided written informed consent, and the study was approved by the local Research Ethics Committee and adhered to the principles of the Declaration of Helsinki.

Procedure

Motion perception was measured with the coherent motion direction identification test before (pretest), two days after (post1-test) and one month after (post2-test) training. The post1-test was conducted two days after training because at least 48 hours of time interval was frequently used in previous studies to limit potential carryover effects of tDCS (Wu, et al., 2021). Tests without tDCS effects contribute to pure improvement in VPL since tDCS itself could directly benefit visual motion perception (Wu et al., 2020). However, participants in the current study required 5 tDCS sessions over the 5-day training sessions. Repetitive tDCS may cause long-lasting effects (Davis & Smith, 2019), but the specific duration of repetitive tDCS is currently unclear. Thus, the coherent threshold was also measured for a longer period after training (i.e., one month) than in previous studies.

After the pretest, participants were trained for 5 consecutive days. In the online tDCS condition, anodal tDCS was applied to the left hMT+ during training. In the offline tDCS condition, participants underwent training immediately after anodal tDCS. In the sham condition, sham tDCS and training were conducted synchronously (Figure 1).

All experimental procedures were completed in a quiet, dark room in which participants were seated in front of a computer screen. The experimental environment was kept constant in all sessions. A gamma-corrected 60 × 34 cm monitor (spatial resolution: 1920 × 1080 pixels; refresh rate: 85 Hz) was used to present experimental stimuli by a computer running MATLAB and PsychToolbox extensions. Participants binocularly viewed the displays from 75 cm away, with their heads stabilized by a chinrest and headrest; the displays covered 6.84°×3.89° of their visual fields. For participants with corrected-to-normal vision, normal VA was ensured by optical correction.

Coherent motion direction identification

During the test phases, participants completed the pre, post1- and post2-tests, each of which contained 120 trials and lasted approximately 4 min. As shown in Figure 2, a 300-ms blank was first presented, accompanied by a brief tone. After that, 400 white moving dots (0.18° in diameter) were presented for 200 ms against a gray background (mean luminance: 26 cd/m^2), with 17 frames, each displayed for 11.76 ms. In the first frame, the moving dots were randomly distributed within the round window (8° in diameter), with a speed of 10°/s. The density constant (7.96 dots/deg^2) was maintained by quickly replenishing the new dots at different, randomly selected locations within the window once the dots moved outside of the window. The coherent dots moved along one of the four directions: 45°, 135°, 225°, and 315°; the other dots moved in random directions. The participants needed to judge the direction of coherent motion with a four-alternative forced-choice (4AFC) by pressing the button on a gamepad. A brief tone appeared after each response regardless of its accuracy, and the next trial started 900 ms after the response. Adequate practice was necessary to ensure familiarity with the test.

An adaptive three-down/one-up staircase method was used to assess the percentage of coherent moving dots (coherent threshold). This method, for which the correct response rate converged to 79.3%, decreased coherence by 10% (multiplying the previous value by 0.9) after every three consecutive correct responses and increased coherence by 10% after every incorrect response. A reversal was recorded once the direction of the staircase changed (changing from decreasing to increasing coherence or vice versa). The first four or five reversals were deleted if the total number of reversals was even or odd, respectively. We averaged the remaining reversals to assess the coherent threshold for detecting the direction of coherently moving dots. The initial threshold (i.e., 30%) was set close to the expected coherent threshold according to the pilot testing.

During the training phase, each participant took part in a 5-day consecutive training period. A brief tone appeared only following each correct response. Each training session included 6 blocks of 80 trials lasting approximately 17.2 ± 0.5 min, which was shorter than the stimulation time (20 min). In other words, participants in the online condition completed the training under stimulation. Even though participants finished the training in advance, they were asked to wait until the completion of the 20-min tDCS session. Participants relaxed between two blocks and decided their own start time for the next block.

In the middle of the training session, participants were asked to report tDCS-induced sensations: what is your sensation of the stimulation region? Sensation intensity was evaluated as follows: 0 = none, 10 = strong and intolerable. The sensations induced by anodal tDCS were perceived more strongly than the sensations induced by sham tDCS independent of online and offline tDCS; moreover, online tDCS was indistinguishable from offline tDCS.

Brain stimulation

The conventional 1 × 1 tDCS over hMT+ requires the active electrode to be placed approximately 3-4 cm above the mastoid-inion line and 6-7 cm to the left or right of the midline in the sagittal plane, and the return electrode is placed at the vertex (Antal et al., 2012; Larcombe et al., 2018). To generate hMT+ more focally, 4 × 1 ring HD-tDCS stimulation (Soterix Medical, NY, USA) was administered. As shown in Figure 3A, the electrode montage used here has been employed in previous research (Zito et al., 2015). The central electrode was placed at PO7, four return electrodes were placed at a distance of approximately 5 cm from the central electrode, and their locations corresponded to P3, OZ, TP7, and PO9 (10–10 standard EEG system). In anodal tDCS, the anode was located at PO7, delivering 20 min of 1.5 mA direct current (fade in/out: 30 s). The other electrodes received an equal return current. Conductive gel was injected into the electrode casings (diameter 1 cm) to increase conductivity and reduce impedance (< 5 kΩ for the duration of the entire session). The polarity of all electrodes in cathodal tDCS was reversed. The current of sham tDCS was ramped up over 30 s at the beginning of the 20 min period and ramped down over 30 s at the end of the period. As shown in Figure 3B, the current flow of anodal tDCS was calculated using HD-Explore software (Soterix Medical Inc., New York).

Since the stimulator was operated by an experimenter, he or she was unblinded to whether the participant was receiving anodal or sham stimulation. However, this experimenter was blinded to the purpose and the experimental design of the current study. Unblinding was performed once data collection was completed prior to analysis.

Data analysis

Total learning = within-session improvements + between-session improvements; the within-session improvements (1) and between-session improvements (2) were then defined as follows (Reis et al.,2009):

$$\sum_{i=1}^{5}(\text{threshold}_{day\ i,\quad last\ block} - \text{threshold}_{day\ i,\quad first\ block}) \tag{1}$$

$$\sum_{i=1}^{4}(\text{threshold}_{day\ i+1,\quad first\ block} - \text{threshold}_{day\ i,\quad last\ block}) \tag{2}$$

RESULTS

Anodal online tDCS over the left hMT+ improved the VPL of coherent motion

The 2 tests (pre and post1) and 3 conditions (online, offline and sham) two-way ANOVA on the coherent threshold was carried out. A significant interaction effect was found (Figure 4A), F (2,33) = 3.35,p = 0.047, $\eta^2 = 0.02$. Post hoc LSD analyses did not show a significant difference for the pretest among the online, offline and sham conditions ($p > 0.1$), indicating successful random grouping. For the post1-test, the coherent thresholds of online tDCS were significantly less than those of offline ($p = 0.001$) and sham tDCS ($p = 0.001$), but the thresholds of offline and sham tDCS were not significantly different ($p = 0.931$). The magnitude of coherent threshold improvements between the pre- and posttest was calculated. A 3-condition (online, offline and sham) one-way ANOVA on the magnitude of improvements showed a significant main effect, F (2,33) = 3.35,p = 0.047, η ^{2} = 0.08. The amount of improvement in response to online tDCS was significantly larger than those in offline (p = 0.031) and sham tDCS (p = 0.033) in post hoc LSD tests. However, there was no obvious difference between the offline and sham conditions (p = 0.985).

Additionally, we analyzed the coherence threshold of the post2-test that was performed one month after training. As shown in Figure 4B, a two-way ANOVA also showed a significant interaction effect, F (2,33) = 3.76, p = 0.034, η ^{2} = 0.02. Further post hoc LSD analyses showed that online tDCS induced a lower threshold in the post2-test than offline tDCS (p = 0.020) and sham tDCS (p = 0.036), and no significant difference in the threshold of the post2-test between offline and sham tDCS was found (p = 0.790). In terms of the degree of threshold change between the pre- and post2-tests, one-way ANOVA also demonstrated a significant main effect,F (2,33) = 3.35, p = 0.047, η ^{2} = 0.08. Furthermore, online tDCS generated larger improvement than offline (p = 0.018) and sham tDCS (p = 0.031). However, there was no obvious difference between offline and sham tDCS (p = 0.815).

In total, anodal tDCS applied synchronously with training induced greater improvement than offline and sham tDCS regardless of the post1- and post2-test results, suggesting that anodal online rather than offline tDCS boosts VPL.

The beneficial effect of tDCS on VPL was not related to changes that occur during training and consolidation

Within-session and between-session improvements were calculated in the current study and were conducive to a deep understanding of the performance changes induced by tDCS. The former are the performance improvements that occurred in a single training session, reflecting the degree of change during training. Correspondingly, the latter are the performance improvements that occurred between training sessions, reflecting the amount of change during the consolidation period (Reis et al., 2009).

First, we established the learning curve (threshold as a function of training blocks) under online, offline and sham tDCS conditions (Figure 5). Second, we investigated the relative impact of tDCS on within-session improvements and between-session improvements. As shown in Figure 6, there was no significant difference in within-session improvements among the three conditions, F (2,33) = 0.93, p= 0.405, η ^{2} = 0.05, or in between-session improvements, F (2,33) = 0.57, p = 0.571,η ^{2} = 0.03. The total learning (the sum of within-session and between-session improvements) was also not different among the three conditions, F (2,33) = 1.25, p = 0.299,η ^{2} = 0.07. The above results indicated that performance improvements during a certain period of time (within and between sessions) were not different among online, offline and sham tDCS.

DISCUSSION

The main result of this study is that anodal online tDCS over the left hMT+, compared with anodal offline and sham tDCS, can improve visual motion perceptual learning after 5-day training sessions. Additionally, this facilitated effect of online tDCS does not occur through the within- and between-session improvements, indicating that tDCS does not change the performance amount during training and consolidation.

We observed a significant enhancement of VPL when anodal online tDCS was applied. VPL has great application prospects to improve or restore vision (Lu et al., 2016). However, adequate improvement after VPL often requires a long duration of training. Thus, the method to enhance VPL is of great scientific and practical significance. tDCS, a noninvasive and safe method to change cortical excitability, has been considered to have potential for improving VPL, but the results thus far are inconsistent. Some studies found a positive effect of tDCS on VPL (Herpich et al., 2019; Karlaftis et al., 2021); however, other studies found no effect or a diverse effect. This study found that anodal tDCS can effectively promote visual performance after training, which has great significance to the application of VPL.

Importantly, online rather than offline tDCS improved VPL. Specifically, a larger performance improvement was found when tDCS was applied during daily training but not when it was applied before training, indicating that the tDCS effects on VPL are closely associated with the timing sequence of the stimulation and training. Indeed, most previous studies that confirmed the facilitated effect of tDCS on VPL employed the synchronous protocol of stimulation and training (Karlaftis et al., 2021; Sczesny-Kaiser et al., 2016). Interestingly, this synchronous protocol has also been confirmed in motor learning (Nitsche et al., 2003; Stagg & Nitsche, 2011). For example, Nitsche et al. initially demonstrated a facilitation effect of 15 min of anodal tDCS (1 mA) that was delivered during the whole course of implicit motor learning. Subsequently, Stagg et al. found that 10 min of anodal tDCS (1 mA) improved the learning rate in an explicit motor task if applied during training but not if applied before training. The above evidence indicates that anodal tDCS should be applied online to generate more benefits regardless of learning in motor or vision fields.

However, Pirulli et al. (2013) found the opposite results in visual orientation discrimination learning. Specifically, anodal tDCS resulted in a significant performance improvement if it was applied before task execution but not when it was applied during the task. Participants completed 5 blocks of training within each session. In contrast, the tDCS in the current study was applied over a 5-day period of training sessions, rather than in a single session, which may explain the opposite results (Larcombe et al., 2018). Learning over multiple sessions requires more complex cognitive processes, such as sleep. VPL has been shown to require posttraining nocturnal sleep (Stickgold et al., 2000) or a nap (Mednick et al., 2003) to be successful. Additionally, sleep improves the inducibility of tDCS-induced neural plasticity and further facilitates perceptual learning (Salehinejad et al., 2021). Nevertheless, the application of anodal tDCS during the early consolidation period increases posttraining orientation discrimination performance when participants remain awake, and decreased performance has been observed when participants sleep at night, indicating that VPL consolidation is sleep dependent (He et al., 2021). Thus, future research should compare the difference in the effect of tDCS on VPL between a simple within-session approach and multiple sessions.

In the current study, we investigated when tDCS-induced performance changes occurred (within-session vs. between-session). We did not find a difference regarding within- and between-session improvements among the three stimulation conditions, indicating that the beneficial effect of anodal online tDCS on VPL is not related to the performance changes during training or after training. In a motor skill learning study, participants had to complete 5 days of motor skill training during the application of anodal tDCS over M1. The results showed that anodal tDCS induced significantly greater total learning than sham tDCS. Additionally, the between-session improvements primarily mediated the greater total learning induced by anodal tDCS (Reis et al.,2009). The motor and visual studies presented inconsistent findings, which may be due to the differences between the two neural systems. Indeed, some results of the motor cortex are always inconsistent with results of the visual cortex (Antal et al., 2006) or other areas (Jacobson et al., 2012). Many factors may explain the different outcomes between stimulation in the motor and visual cortex, such as the difference in neuroanatomy and functional anatomy that may induce differential current diffusion (Pirulli et al., 2013; Richard et al., 2015).

We speculated that the beneficial effect of tDCS on VPL may come from the direct effect of tDCS. Specifically, previous studies have demonstrated that even without being combined with training, just a 20-min tDCS session (or one-time tDCS) can improve visual motion perception (Battaglini et al., 2017; Wu et al., 2020). In this case, it is reasonable to assume that tDCS was also able to improve performance during the whole training process, since the VPL was made up of multiple repetitive trainings. As shown in Figure 5, online tDCS decreased the threshold in the first block of the first session, indicating the fast effect of tDCS. After that, the thresholds were reduced until the end of training. Although tDCS was applied during the training period, the thresholds of the posttest were still reduced even if they were measured without stimulation. This result seems to suggest that once visual performance is improved by some methods (e.g., tDCS) during training, the heightened performance is maintained even if the method is no longer actively being applied.

The neural mechanisms underlying the tDCS-induced facilitation of VPL may be explained by the change in neurotransmitters. Anodal tDCS has been shown to be excitatory (Antal et al., 2004b; Nitsche & Paulus, 2000), resulting in decreased inhibitory transmission (i.e., GABA) in visual (Barron et al., 2016), frontal (Harris et al., 2019) and motor areas (Bachtiar et al., 2015; Kim et al., 2014). Additionally, decreased GABA levels are related to improved perceptual learning (Baroncelli et al., 2011; Frangou et al., 2018). Thus, it is possible that anodal tDCS facilitates learning by decreasing local GABA levels. Indeed, anodal tDCS has been shown to decrease local GABA levels and change functional connectivity and further facilitate visual (Karlaftis et al., 2021) or motor learning (Bachtiar et al., 2015; Stagg et al., 2011).

We found stronger sensation induced by anodal tDCS than sham tDCS across all training sessions. Indeed, many previous studies also found a difference in subjective feelings between active and sham tDCS (Ambrus et al., 2010; Larcombe et al., 2018). We believe that participants do not take training more seriously and do not proceed more carefully, even if they perceive a stronger sensation induced by real tDCS. This is due to the between-subjects design of this study. Participants in one group only received one type of tDCS during the whole experiment; therefore, they did not experience different stimulations and could not judge which was real stimulation or which was sham stimulation.

Notably, only anodal tDCS was considered in the current study. Thus, the interesting question is whether cathodal tDCS of the left hMT+ can also improve coherent motion learning with this type of multisession training protocol. Antal et al. (2004b) found that cathodal rather than anodal tDCS of the hMT+ improved the percentage of correctly tracked movements. Additionally, Battagliniet et al. (2017) found that both anodal and cathodal tDCS increase coherent motion discriminability. These studies seem to indicate that cathodal tDCS of hMT+ also affects the identification of coherent motion. Similarly, the left hMT+ rather than the right hMT+ was stimulated in this study. Only one study found a significant improvement in motion perception after cathodal tDCS over the right hMT+ (Zito et al., 2015). Most studies stimulated the left hMT+ and found a beneficial effect of tDCS on motion perception (Battagliniet et al., 2017; Wu et al., 2020). These results suggest that both the left and right hMT+ may be effective stimulation targets to improve motion perception. We chose anodal tDCS to stimulate the left hMT+ since this polarity of stimulation and cerebral hemisphere have been the subject of more investigations, especially on the effect of tDCS on perceptual learning, allowing a comparison of the results with those of previous studies.

From a practical perspective, tDCS contributes to translating VPL to applications. VPL has been regarded as a potential treatment for various low vision issues. Inadequate training makes it difficult to achieve the desired training effect; thus, we expect to obtain maximal gains with minimal costs. Therefore, it is important to look for effective ways to promote VPL. The current study found that anodal online tDCS has a beneficial effect on the amount of visual improvement after the 5-day training period, which provides empirical support for effective ways to improve VPL. However, participants in the current study only trained in a limited time (5 days), and the visual performance has not yet reached a plateau. Therefore, we cannot draw a conclusion that tDCS is able to ultimately improve the learning effect (magnitude of improvement) or just increase learning within a limited time. This problem warrants further study.

CONCLUSION

In summary, anodal tDCS can improve VPL. Additionally, a larger improvement was found only when anodal tDCS was applied during training but not when anodal tDCS was applied before training, indicating that the time sequence of stimulation and training influences the effect of tDCS on VPL. Finally, within- and between-session improvements were not different among online, offline and sham tDCS, suggesting that the facilitated effect of tDCS on VPL is not related to the performance changes during the training or consolidation period. These findings suggest that tDCS may be a potential method to enhance VPL, but the stimulation protocol should be considered in practical applications.

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CONFLICT OF INTEREST

The authors report no conflict of interest.

AUTHOR CONTRIBUTIONS

All authors contributed to designing the study. Di Wu and Pan Zhang designed the experiment. Yifan Wang collected the data. Di Wu, Kewei Sun and Panhui Wang performed statistical analyses and visualization. Di Wu and Wei Xiao wrote and revised the manuscript. Na Liu and Wei Xiao guided and supervised the study. All authors discussed the results and contributed to the final manuscript.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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FIGURE 1 Experimental procedure. The experiment included the following conditions with a between-subjects design: anodal online tDCS, anodal offline tDCS and anodal online sham. In the online tDCS group, tDCS was applied while participants underwent training; in the offline tDCS group, tDCS was applied before training began. The black rectangles represent the three tests of motion direction identification that were conducted before (pretest), 2 days after (post1-test) and one month after (post2-test) training. The white rectangles denote the 5-day training sessions. The yellow arrows represent the time of stimulation.

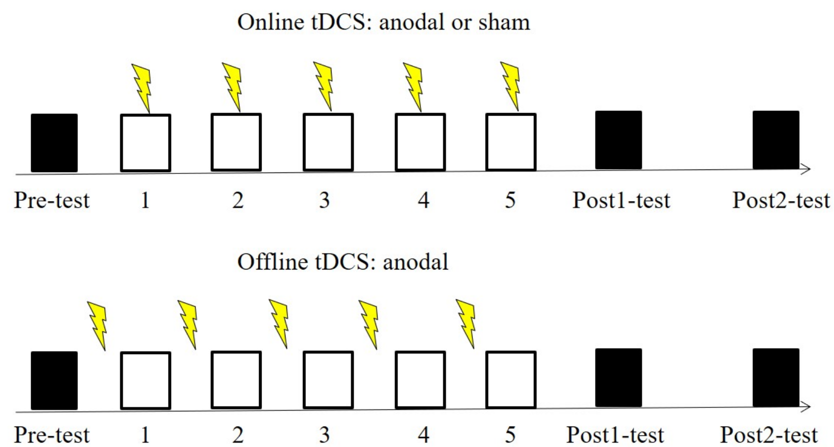
FIGURE 2 Schematic illustration of a typical trial in coherent motion direction identification tasks.

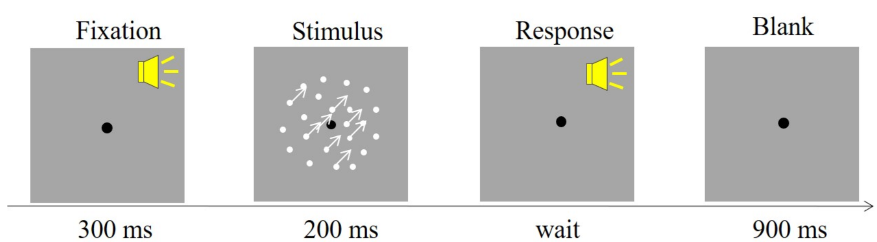
FIGURE 3 Electrode montage and simulated distribution of the electrical field. (A) The central electrode (red point) was placed over PO7; the four return electrodes (blue points) were placed over P3, OZ, TP7 and PO9. (B) The field intensity and current flow for anodal HD-tDCS were modeled with HD-Explore software (a) coronal view; (b) sagittal view; (c) axial view.

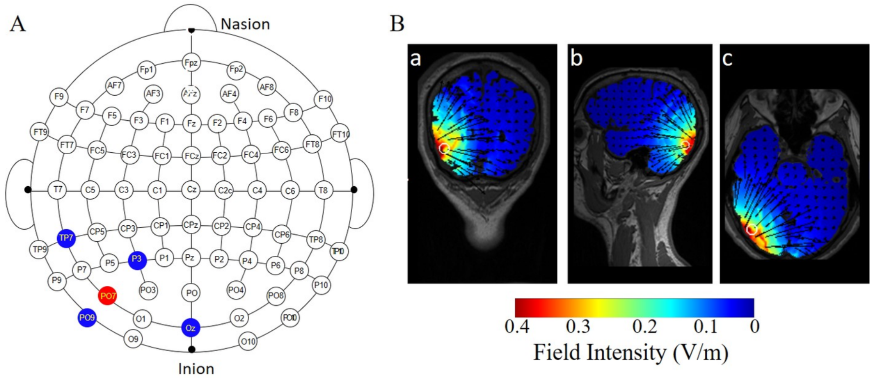
FIGURE 4 Pre- and posttest results. (A) The post1-test was conducted 2 days after training. (B) The post2 test was carried out one month after training. Data show the mean (bars) ± SEM.**, $p < 0.01$; *,$p < 0.05$.

FIGURE 5 The learning curve for anodal online (red solid circles), offline (green diamonds) and sham (gray hollow circles) tDCS conditions. (A) Threshold as a function of 30 training blocks over 5 days. Each block describes the group mean of the average number of 80 trials in each block. The dotted lines represent intervals between consecutive days.

FIGURE 6 Within- and between-session improvements. Within-session improvements (horizontal stripe), between-session improvements (vertical stripe) and total learning (solid) in the online tDCS (red), offline tDCS (green) and sham tDCS (gray) conditions are shown.






A
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a
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0.4
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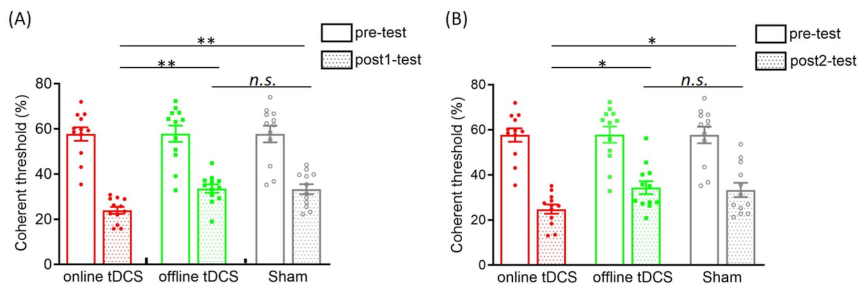
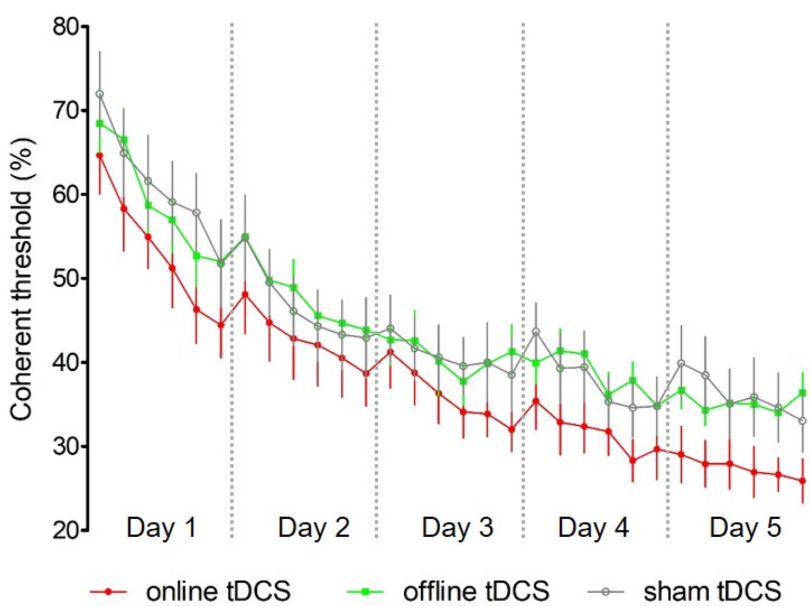
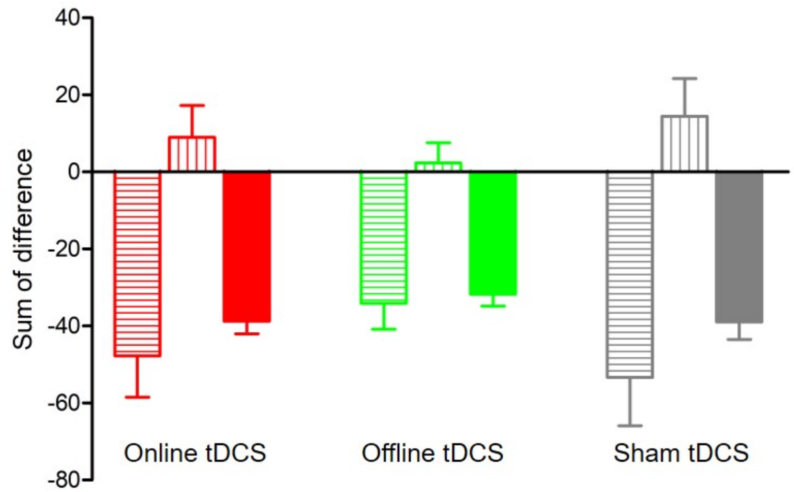
Field Intensity (V/m)


(A)
(B)
pre-test
post1-test
post2-test
Coherent threshold (%)
n.s.
online tDCS
offline tDCS
Sham


Coherent threshold (%)
Day 1
Day 2
Day 3
Day 4
Day 5
online tDCS
offline tDCS
sham tDCS



Sum of difference
40
20
0
-20
-40
-60
-80
Online tDCS
Offline tDCS
Sham tDCS