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

Abbreviated title: Comparing multiple types of tES in modulating VPL

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Abstract

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 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,

subjects' occipital region 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 performing

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 terms of

learning rate and performance improvement, while there was little modulatory effect

in the anodal tDCS condition. Remarkably, the 10 Hz tACS condition exhibited

superior modulatory effects to 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.

Keywords: transcranial electrical stimulation, tDCS, tACS, tRNS, visual perceptual

learning, visual plasticity, unsupervised learning, implicit learning

Introduction

Our visual system is remarkably malleable (i.e., visual plasticity) throughout the entire lifespan, 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 (NIBS) techniques (He *et al.*, 2022a). 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 *et al.*, 2022a). More importantly, VPL has been widely applied in various fields (Lu *et al.*, 2016), such as low-vision rehabilitation (Huang *et al.*, 2022; Levi *et al.*, 1996), remediation for dyslexia (Gori *et al.*, 2014; Meng et al., 2014), X-ray security screening (McCarley *et al.*, 2004), sports and military training (Hadlow *et al.*, 2018), and medical imaging education (Alexander *et al.*, 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. There are three most common types of tES techniques categorized based on the current waveform, i.e., transcranial direct current stimulation (tDCS) (Nitsche *et al.*, 2000; Priori *et al.*, 1998), transcranial alternating current stimulation (tACS) (Antal *et al.*, 2008), and transcranial random noise stimulation (tRNS) (Terney *et al.*, 2008). All 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 *et al.*, 2001; Potok *et al.*, 2023), visual acuity (Bocci et al., 2018; Reinhart *et al.*, 2016), motion direction discrimination (Battaglini *et al.*, 2023; Ghin *et al.*, 2018), and peripheral target identification in a crowded environment (Battaglini et al., 2020; Chen *et al.*, 2021),

therefore establishing causal links between brain activity and cognitive functions

(Zhang *et al.*, 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 *et*

al., 2021; He *et al.*, 2022a; He *et al.*, 2022b; Wu *et al.*, 2023; Yang *et al.*, 2022). From

the prospective of translational applications, trainees aspire to attain the greatest

training benefits in the briefest timeframe. Whereas, in a typical practical-oriented

application case, thousands of trials across multiple training sessions are required

usually. Boosting VPL by tES is expected to accelerate learning and make subjects

obtain greater benefits (He *et al.*, 2022b; Herpich *et al.*, 2019), which was aligned

with trainees' expectations.

Different types of tES have been adopted to modulate VPL (for a review, see He

et al., 2022a). Concerning the effect of tDCS on modulating VPL, the results are

mixed yet, and that no consistent result has been found regardless of whether tDCS

was administered before task execution (offline mode) or during task execution

(online mode). For instance, when tDCS was applied during task execution, anodal

tDCS were found to be effective in boosting VPL in some studies (Frangou *et al.*,

2018; Wu *et al.*, 2022b), while in other studies no obvious modulatory effect was

found (Fertonani *et al.*, 2011; Herpich *et al.*, 2019; Larcombe *et al.*, 2018a; Larcombe

et al., 2018b; Wu *et al.*, 2022a) and even a suppressive effect was observed (Jia *et al.*,

2022b). Studies using offline tDCS in VPL task showed similarly conflicting results

(Pirulli et al., 2013; Pirulli et al., 2013;Wu *et al.*, 2023;). By contrast, the results of

modulating VPL by tRNS is relatively consistent. Specifically, high-frequency

(100-640 Hz) tRNS boosts VPL effectively in both healthy and clinical populations

(Camilleri *et al.*, 2014; Campana *et al.*, 2014; Cappelletti *et al.*, 2015; Conto *et al.*,

2021; Donkor *et al.*, 2021). With regard to tACS, though the underlying neural

mechanisms of action of tACS on the brain are relatively clear among tES techniques

(Johnson *et al.*, 2020; Krause *et al.*, 2019; Zaehle *et al.*, 2010), only limited studies

have been conducted to modulate VPL. Specifically, 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 in other

stimulation frequencies (e.g., 6, 20, and 40 Hz) (He *et al.*, 2022b). Similarly, in

another study, occipital 3 Hz tACS was found to show little effect on VPL

(Zizlsperger *et al.*, 2016). Moreover, we also found that the modulatory effect of 10

Hz tACS was absent when other cortical areas were stimulated (He *et al.*, 2022b).

Altogether, these studies demonstrate that tACS facilitates VPL in a frequency- and

location-specific manner.

Despite advancements in VPL were observed following the application of

diverse types of tES, there still lacks a systematic evaluation of the modulatory effects

of tES on VPL. Notably, studies on modulating VPL by tES usually employ a

relatively small sample size design, which might suffer the risk of sampling bias and

limit the generalizability of those findings (Minarik *et al.*, 2016). To this end, 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 approximately

30 participants in each group, which provides 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 (He *et al.*, 2022b), and all data for the 10 Hz tACS condition and the sham 10 Hz tACS condition in that study (He *et al.*, 2022b) were included in the present study. A screening questionnaire was administered 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 seven hours per night over the last two weeks, 4) during ovulation phase of the menstrual cycle or pregnancy (He *et al.*, 2019; He *et al.*, 2022b). All experimental protocols and procedures were approved were approved by the Ethics Committee of the School of Psychological and Cognitive Sciences at Peking University. Before participation, an informed written consent was obtained from each subject.

Apparatus and Stimulation protocol

MATLAB (R2015a, MathWorks, Natick, MA) and Psychotoolbox-3 extensions (Brainard, 1997) were used to generate and control visual stimuli, which were presented on an LCD monitor (Display□+□+, Cambridge Research Systems, UK)

with a grey 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. Subjects' heads were fixed by a chin-and-head rest at a

viewing distance of 70 cm. To ensure that subjects' eye positions were stable within 1°

from the fixation point when visual stimuli were presented, the Eyelink1000 plus

eye-tracking system (SR Research Ltd., Ontario, Canada) was used to monitor

subjects' eye movement throughout the whole 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 GmbH, Ilmenau, Germany), through a pair of rubber electrodes of 5×7

cm^2. The electrodes were inserted into two soaked sponges (0.9% saline solution) and

attached to the subjects' scalp by two elastic bandages. The current intensity was

constant 2.0 mA for anodal tDCS, while 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 were 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 set used in this study were the same as our

previous studies (He *et al.*, 2021; He *et al.*, 2022b). Oriented Gabor patches with noise

(diameter = 1.25°; spatial frequency = 3.0 cycle/°; Michelson contrast = 0.5; standard

deviation of Gaussian envelope = 0.42°; random spatial phase; 25% 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° + θ appeared 100 ms each in a random order with a 500-ms blank

interval (**Fig.1**(A)). 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 (counter-clockwise or clockwise) by pressing keys.

Subjects' orientation discrimination threshold at 75% accuracy was estimated using a

QUEST staircase procedure, such that the θ varied trial by trial (Watson *et al.*, 1983).

Subjects would have a rest after each staircase. No feedback was provided in all test

and training sessions.

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

counter-clockwise), while gazing at the central fixation point. There was no feedback

after each trial. (B) Experimental protocol. Subjects underwent a pre-training test, five

daily training sessions, and a post-training test. The pre-training 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) were 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 denoted the anodal electrode and cathodal electrode,

respectively. These head models were generated by FaceGen Modeller (version 3.4).

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 session, a test session was conducted,

respectively, i.e., the pre-training test (Pre) and the post-training test (Post) (**Fig.1** (B)).

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

presented was stimulated. Two electrodes were placed over subjects' visual cortex and

the vertex (i.e., O2 and Cz in the international 10-20 EEG system, respectively;

Fig.**1**(C)). Electrical stimulation was delivered concurrently with training with a

ramp-up of 30 s 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 (*pre-training*

threshold − post-training threshold)/*pre-training threshold ×100%*. All estimated

thresholds were then normalized: the estimated threshold for each session was divided

by the estimated threshold at Pre, 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 threshold across all sessions using a power

function:

$$225 \qquad \log_{10}(\mathrm{Th}(t)) = \rho \times log10(t)$$

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 (BH) to control

false discovery rate (FDR) 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 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 between 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. 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 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. Further analyses showed that the thresholds at Post were lower than those

at Pre for all stimulation conditions (sham: $t(25) = 4.33$, $p_{adj} < 0.001$, Cohen's $d = 0.85$;

tDCS: $t(25) = 6.77$, $p_{adj} < 0.001$; *Cohen's d = 1.33*; tRNS: $t(25) = 10.21$, $p_{adj} < 0.001$,

Cohen's d = 2.00; tACS: $t(25) = 9.01$, $p_{adj} < 0.001$, *Cohen's d =1.77*). 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.

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: 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 (standard error of the mean) across subjects

Learning rate was modulated by tES

The efficiency of performance improvement in learning is typically quantified by learning rate. We examined learning curve differences between different stimulation conditions. A one-way ANOVA revealed that the main effect of *Condition* on learning rate (ρ) 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. 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), while the learning rates in both the tRNS and the tACS conditions

were significantly greater than that in the sham condition (tRNS vs. sham: $t(50) =$

2.90, $p_{adj} = 0.01$, *Cohen's d = 0.80*; tACS vs. 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 rate in the tACS condition was higher than that in the tRNS condition ($t(50)$

$= 2.27$, $p_{adj} = 0.04$, *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 performance improvement differences between

different stimulation conditions. Performance improvement between stimulation

conditions was significant, which was revealed by a one-way ANOVA ($F_{(3,100)} = 9.69$,

$p < 0.001$, $\eta_p^2 = 0.23$). Further analyses showed that the percent improvement in the

10 Hz tACS condition was significantly higher than those in all other stimulation

conditions (tACS vs. sham: $t(50) = 4.85$, $p_{adj} < 0.001$, *Cohen's d = 1.35*; tACS vs.

tDCS: $t(50) = 3.08$, $p_{adj} = 0.008$, *Cohen's d = 0.85*; tACS vs. tRNS: $t(50) = 2.33$, $p_{adj} =$

0.04, *Cohen's d = 0.65*). Notably, the performance improvement in the tRNS

condition was significantly higher than that in the sham condition ($t(50) = 3.55$, $p_{adj} =$

0.003, *Cohen's d = 0.98*). All other differences among the stimulation conditions were

not significant (tDCS vs. sham: $t(50) = 1.74$, $p_{adj} = 0.11$, *Cohen's d = 0.48*; tDCS vs.

tRNS: $t(50) = 1.60$, $p_{adj} = 0.12$, *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. While the modulatory effects of tES on VPL were strongly

dependent on the stimulation type. Specifically, anodal tDCS applied during executing

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 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, while 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 to all previous studies

investigating the modulatory effects of tES on VPL, the present study has the largest

sample size (~30 subjects per condition), and thus ensuring sufficient statistical power

for between-condition comparisons. In short, our findings will provide guidance for

translational applications of combing VPL and tES, and will also provide insights into

neural mechanisms of VPL.

327   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 *et al.*, 2019; Herpich *et al.*, 2019; Larcombe *et al.*,

2018a; Larcombe *et al.*, 2018b; Wu *et al.*, 2022a). 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 *et al.*, 2016; Wu *et al.*,

2022b), or even impairing VPL with a short training session (Grasso *et al.*, 2021;

Grasso *et al.*, 2020; Jia *et al.*, 2022a; Learmonth *et al.*, 2015). The discrepancy

between these studies mentioned above can be caused by many factors, such as

training tasks, training regimes, and stimulation settings. Of note, a small sample size

was adopted in previous studies, which may bias 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

stimulation applied. Previous studies found that anodal tDCS applied prior to task

execution (i.e., the offline mode) was effective in boosting VPL (Pirulli *et al.*, 2013),

while no such modulatory effect was found when anodal tDCS was administrated

during perform the orientation discrimination task (i.e., the online mode) (Pirulli *et al.*,

2013), just like the finding in the present study.

347   We found that high-frequency tRNS was effective in boosting VPL, which is

consistent with previous studies (Camilleri *et al.*, 2016; Camilleri *et al.*, 2014;

Contemori *et al.*, 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). Additionally,

application of high-frequency tRNS led to a decrease in blood oxygenation level

dependent (BOLD) responses during task execution (Chaieb *et al.*, 2009; Saiote *et al.*,

2013), and reduced hemodynamic response (e.g., the amplitude of HbO2 and HbT

responses) (Snowball et al., 2013). Considering that the BOLD responses are

negatively correlated with alpha/beta band power typically (Bastos *et al.*, 2015; Pang

et al., 2018; Scheeringa *et al.*, 2016), which is highly correlated with spatial attention

(Clayton *et al.*, 2015; Kelly *et al.*, 2006), it is reasonable to speculate that

high-frequency tRNS applied during training could increase alpha/beta band power

and consequently boost learning by strengthening top-down modulation (Clayton *et

al.*, 2015; Conto *et al.*, 2023).

We found that occipital 10 Hz tACS boosted VPL efficiently, which was

consistent with our previous study (He *et al.*, 2022b). 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 made subjects learn to discriminate the orientations of task stimuli faster and

achieve a greater improvement, compared with the sham 10 Hz stimulation condition;

further, 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 *et al.*, 2022b). 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 *et al.*, 2015; Michael *et al.*, 2023).

Further, we also found that occipital 10 Hz tACS showed a stronger modulatory

effect than occipital tRNS. It should be pointed out that this study is the first

investigation 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. In contrast, high-frequency tRNS may modulate attentional processing in a

relatively indirect manner, such as by attenuating BOLD response. 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 called the **efficacy of attention hypothesis**. Alternatively, we

speculate that the power produced by these stimulation techniques cause the observed

modulatory effects here. We propose that VPL can only be modulated by external

electrical fields within a certain power range. If the power of a given stimulation falls

outside of this range, it will not be effective in modulating VPL. Conversely, when the

power is optimized, it produces the best modulatory effects. In this context, both 10

Hz tACS and high-frequency tRNS generate power within the range capable of

modulating VPL, but the power generated by 10 Hz tACS is closer to the optimal

range, and thus the former is more efficient in modulating VPL. This explanation is

called the **power of stimulation hypothesis**. It needs to be emphasized that both the

efficacy of attention hypothesis and the power of stimulation hypothesis need to be

examined in the future.

Our findings will provide a practical guide for vision rehabilitation. VPL has

been widely adopted to restore low-vision in neuro-ophthalmology (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 *et al.*, 2022a). However, in a typical

clinic-oriented study, weeks to months of training are required, consisting of

thousands of trials, which is a significant economic and psychological burden on both

the patients' family and the wider society (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 showed that 10 Hz tACS

over visual areas during training accelerated the learning process and maximized

learning gains in healthy adults, which is expected to be significant in 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 (Wu *et al.*, 2023),

and further studies will help to fully understand the effectiveness of this method for

patients.

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(A)

| 500 ms | 100 ms | 500 ms | 100 ms | Response |

(B)

Pre   Post

| Day | 1 | 2 | 3 | 4 | 5 | 6 | 7 |

☐ Test
■ Training
⚡ TES

(C)

tDCS   HF-tRNS   10 Hz tACS   Sham 10 Hz tACS

Current (mA)

30 s / ~27 mins   30 s / ~27 mins   30 s / ~27 mins   30 s / 15 s / 30 s