Transcranial Direct Current Stimulation over the Posterior Parietal Cortex Increases Nontarget Retrieval during Visual Working Memory

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Abstract

Visual working memory (VWM) requires precise feature binding. Previous studies have revealed a close relationship between the posterior parietal cortex (PPC) and feature binding during VWM; this study further examined their causal relationship through three transcranial direct current stimulation (tDCS) experiments. In Experiment 1 (N= 57), participants underwent three sessions of tDCS separately, including PPC stimulation, occipital cortex stimulation, and sham stimulation, and completed delayed estimation tasks for orientations before and after stimulation. Results showed that tDCS over PPC selectively prolonged recall response time (RT) and increased the probability of nontarget responses (a.k.a. failure of feature binding. pNT). In Experiment 2 (N= 29), combining metacognition estimation, we further investigated whether the effects of PPC stimulation were attributed to misbinding (i.e., participants self-reported "remembered" in nontarget responses) or informed guessing trials (participants self-reported "forgotten" in nontarget responses). We replicated the main findings in Experiment 1 and observed greater tDCS effects of PPC on RT in informed guessing trials while there are comparable effects on pNT in these two types of trials. In Experiment 3 (N = 28), we then examined whether the tDCS effects over PPC specifically influenced the memory retrieval process by using a change detection task. We found that PPC stimulation did not influence the recognition RT or accuracy. Together, this study provided direct causal evidence supporting the specific involvement of PPC in feature binding during WWM retrieval, from both aspects of speed and response preference, expanding our understanding of the neural basis of feature binding in VWM.

Key words: content–context binding; occipital cortex; posterior parietal cortex; transcranial direct current stimulation; visual working memory

Significance Statement

Visual working memory (VWM) enables humans to temporarily store and process visual information, which requires accurate binding of items to their unique context. Accumulating studies posited that the posterior parietal cortex (PPC) is closely related to this binding process, the current study further examined their causal relationship. Through three strictly within-subject well-designed noninvasive neural stimulation experiments, we found that PPC stimulation selectively increased response time and binding error during VWM. Moreover, we found these changes were modulated by individual meta-cognition and only occurred during memory recall instead of recognition. Together, our results provided strong evidence that PPC is causally involved in the binding process during VWM retrieval.

Introduction

Visual working memory (VWM), a process of storing and processing visual information temporarily, is an essential basis of higher-level cognitive processes (Baddeley and Hitch,

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*S.Y. and M.W. are co-first authors. Continued on next page. 1974). Precise content-context binding is critical for multi-item VWM. An interference model indicates that VWM capacity is mainly limited by the binding interference between the content of multiple items and their context information (Oberauer and Lin, 2017). Moreover, impaired binding ability is a typical symptom in varying neurodegenerative disorders (Mayer et al., 2012; Kirova et al., 2015). Thus, understanding the mechanism underlying content-context binding in VWM is always an important theoretical question.

Increasing studies have demonstrated the relationship between posterior parietal cortex (PPC) activity and feature binding during VWM. In early studies, patients with right PPC lesions exhibited a decreased accuracy in tasks requiring multi-item bindings (Ashbridge et al., 1999) and reported illusory feature conjunctions during recall (Braet and Humphreys, 2009). Although earlier functional magnetic resonance imaging (fMRI) and electroencephalograph (EEG) studies have revealed that PPC activity was tightly correlated with the number of items kept during VWM (Todd and Marois, 2004), recent fMRI studies showed that holding the memorized items constant, PPC activity was higher when binding demands increased, suggesting that PPC played a closer role in the binding process (Gosseries et al., 2018; Cai et al., 2020).

Besides, modeling studies have advanced the relationship between PPC and feature binding to the individual and trial level. Bays et al. (2009) proposed a multiple-component mixture model to estimate individuals' probability of nontarget responses, which reflected the failure of binding in a delayed estimation recall task. Accordingly, Cai et al. (2020) found that the neural decoding strength of the context information (i.e., location) in PPC predicted nontarget response rates. Moreover, Schneegans and Bays (2016) proposed a novel model to estimate the probability of nontarget recalls at the trial level. Combining this model and metacognitive reports, researchers further identified two types of nontarget responses that reflect different cognitive processes (Pratte, 2019). In the misbinding condition, individuals are unconscious of recalling a nontarget item and report a high recall confidence (i.e., "remember trials"). In the informed guessing condition, in contrast, they know they may wrongly report a nontarget item and thus report low recall confidence (i.e., "forgotten trials"). Recently, Mallett et al. (2022) observed that participants responded with high confidence in about three-quarters of nontarget trials in a delayed estimation task. More importantly, they found that nontarget items could be decoded in PPC since early maintenance. Unfortunately, this study did not compare the differences between these two types of nontarget responses; thus the involvement of PPC in different nontarget responses was still unclear.

Transcranial direct current stimulation (tDCS) is a noninvasive neuromodulation technique to explore the causal relationship between neural activities and cognitive processes. Typically, tDCS involves a two-electrode setup on the scalp to deliver weak direct current, with the anodal stimulation increasing cortical excitability while the cathodal stimulation inhibiting the excitability (Nitsche and Paulus, 2000; Stagg and Nitsche, 2011). Currently, tDCS research testing the relationship between PPC and VWM has focused on memory capacity, while the results were quite controversial (Li et al., 2017; Wang et al., 2019; Dumont et al., 2021; Jiang et al., 2023). For these inconsistencies, researchers have proposed some important individual differences modulating tDCS effects, such as the VWM baseline (Tseng et al., 2012; Hsu et al., 2014), remember-subset strategy (Wang et al., 2020), and biorhythms (i.e., morning vs afternoon; Salehinejad et al., 2019; 2023). In sum, few tDCS studies have examined the causal relationship between PPC and feature binding, and to answer this question, it is critical to control irrelevant variables and consider potential individual differences that affected tDCS effects.

In this study, we systematically investigated the causal relationship between PPC and feature binding in VWM through three tDCS experiments. In Experiment 1, combined with the three-factor mixture model, we examined the effect of tDCS over PPC on binding process in a delayed estimation task and explored whether individual differences in capacity and recall strategies affected tDCS effect. In Experiment 2, we tried to replicate the results of Experiment 1 and further investigated the involvement of PPC in two types of nontarget responses (i.e., misbinding and informed guessing), by integrating remembered-forgotten self-reports. In Experiment 3, we examined whether the tDCS effects specifically during memory retrieval by using a change detection task (e.g., recognition) instead of a delayed estimation task (e.g., recall). If tDCS changed VSTM maintenance, similar effects should be observed in both tasks; otherwise, no such effect would be detected in the recognition task.

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Materials and Methods

Experiment 1

Participants. Fifty-eight university students participated in Experiment 1 [34 females; mean (M), 20.10 years; SD, 1.40]. All participants were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological or psychiatric disorders. Before the experiment, participants signed a written informed consent required by the institutional review board of the Department of Psychology and Behavioral Sciences, Zhejiang University. Participants received monetary compensation for participation (¥30 per hour).

Experimental procedure. We modified a delayed estimation task for orientations from previous studies to estimate the tDCS effects on the feature binding process in VWM, and only high memory loads were included given researchers have reported higher chances of tDCS effects in the super-capacity condition (Wang et al., 2019, 2020). In each trial, after a 500 ms white central fixation $(0.75 \times 0.15^{\circ})$, an array of six or eight white, randomly oriented bars $(2 \times 0.3^{\circ})$ were presented for 200 ms. All bars were uniformly presented on an invisible circle (centered on the screen, radius of 6°), and orientations of these stimuli were randomly selected from 10 to 170° with at least 10° apart. After a 1 s delay, participants were instructed to recall the orientation of the bars at the probed position as precisely and fast as possible, by moving the mouse and clicking the left bottom on the white circular probe (radius of 2°). The maximum response time (RT) was 8 s. Participants completed the task before and after each tDCS session for ~20 min. Each session consisted of 240 trials which were divided into four blocks, with two memory loads randomly mixed. Participants completed 24 practice trials in each memory load condition before the formal experiment to become familiar with the task.

Experimental stimuli were displayed on a 17 in color screen running MATLAB 2019a (MathWorks) and the Psychophysics Toolbox 3.0.12 (Brainard, 1997). Participants were seated 60 cm away from the monitor (resolution, 1,920 × 1,080; refresh rate, 60 Hz) in a quiet room and were instructed to keep their eyes fixed on the center of the screen throughout the experiment. At the end of the experiment, participants completed a five-point scale to evaluate how often they use remember-all strategy or remember-subset strategy under different memory loads (1, always "remember-all"; 5, always "remember-subset").

tDCS setup. Participants underwent three tDCS sessions, including PPC stimulation, occipital cortex (OCC) stimulation, and sham stimulation. The order of stimulations was counterbalanced across participants, and three stimulations were performed separately with an exactly 48 h interval to minimize potential carryover effects and influences of circadian rhythms (Fig. 1*B*). tDCS was delivered by the DC-STIMULATOR MC device (neuroConn) using a pair of plastic electrodes (5 × 7 cm²) in a saline-soaked synthetic sponge. In PPC stimulation, the anodal electrode was placed over P4 according to the international 10–20 EEG electrode system (Hsu et al., 2014; Li et al., 2017; Wang et al., 2019, 2020), the reference electrode was placed over the left cheek. Then a 20 min, 2 mA current was applied, with a linear fade in and fade out of 30 s which could minimize the uncomfortable feelings of sudden current changes. The choice of stimulation parameters referred to previous studies and guaranteed long-lasting stimulation effects during the poststimulation task (Wang et al., 2019, 2020). In OCC stimulation, the only difference is the anodal electrode was placed over Oz (Makovski and Lavidor, 2014; Li et al., 2017). For the sham condition, the anodal electrode was randomly placed over P4 or Oz, and the stimulation was only delivered within the first and last 30 s to simulate the itching feelings during active stimulation. During all stimulations, participants sat and took a rest. The current density distributions for tDCS settings were presented using COMETS, an open-source toolbox based on MATLAB (http://www.cometstool.com; Lee et al., 2017; Fig. 1*C*).

Data analysis

Estimations of behavioral performance. We calculated the RT and the recall error under different memory loads. RT was defined as the duration between the cue onset and response confirmation, and the recall error was obtained as the angular distance between the reported orientation and the targeted orientation. Then, we adopted the three-factor mixture model (Bays et al., 2009) and fit the distribution of raw errors to obtain the precision of target responses (κ), the probability of target responses (pT), the probability of nontarget responses (pNT), and the probability of guess responses (pU). Among these measures, a higher pNT indicated a higher probability of content–context binding errors. Memory capacity was calculated as pT × memory load according to previous research (Zhang and Luck, 2008). One participant was excluded due to poor working memory performance (capacity <1). Then, 57 participants were included for further analysis.

Estimations of tDCS effects. To examine tDCS effects, we first compared the behavioral parameters between active stimulation (PPC or OCC stimulation) and sham stimulation separately. For each behavioral parameter, we conducted a three-way repeated-measure analysis of variance (ANOVA) of stimulation condition (active vs sham), test time (pretest vs posttest), and memory load (Set Size 6 vs Set Size 8). If interaction effects were significant, we then performed two-way repeated-measure ANOVAs investigating the tDCS effects under each load. Furthermore, if any tDCS effect was significant in active stimulation, we tested whether this effect was region-specific by comparing tDCS effects over PPC and OCC with repeated-measure ANOVAs as well as calculating Pearson's correlation between PPC and OCC tDCS effects (i.e., the behavioral changes before and after stimulation). We reported *p* values, effect size, and Bayesian factor (BF) for all statistical analyses.



Figure 1. *A*, Schematic diagrams of the delay estimation task. *B*, tDCS procedures. *C*, The placement of tDCS electrodes (left) with red patches representing the anodal electrode (P4 and Oz) and a blue patch representing the reference electrode (left cheek) and cortical current density distributions from an overhead view (right).

Examination of influence factors of tDCS effects. For significant tDCS effects at the group level, we examined the potential influences of individual working memory capacity and recall strategy scores on tDCS effects via Pearson's correlation analyses. Because the capacity measures (i.e., $pT \times each$ memory load) were highly correlated in three prestimulation sessions and two memory loads (rs > 0.379; ps < 0.01; BF_{10s} > 10.263), we averaged them as the individual capacity performance. The recall strategy scores were obtained in each memory load, and as expected, there was a higher chance of using the remember-subset strategy in higher memory load conditions [SS6, M (SD), 4.158 (0.841); SS8, M (SD), 3.368 (1.063); difference, $t_{(56)} = 6.926$; p < 0.001; BF > 1,000]. Similarly, the recall strategy scores across set sizes were highly correlated (r = 0.613; p < 0.001; BF₁₀ > 1,000), we then averaged them as the individual memory strategy if the tDCS effects were significant in both set sizes, while only using the recall strategy score in the specific memory load (i.e., Set Size 8) if the tDCS effect was load-specific.

Experiment 2

Participants. The sample size was determined using G*Power 3.1 (Faul et al., 2007) based on the effect size of increased *p*NT after PPC stimulation in Experiment 1 ($\eta_p^2 = 0.119$). A minimum sample of 28 participants was required to achieve a power of 90%, with a significance level of 0.05. We recruited 33 healthy university students (14 females; M, 23.10 years; SD, 2.70), and four participants were excluded due to poor task performance, resulting in a final sample of 29 in this experiment. Recruitment and payment criteria were consistent with Experiment 1.

Experimental procedure and tDCS setup. The task procedure was similar to Experiment 1, except that participants were required to make metacognitive evaluations of their recall during the task. This design could help us to distinguish misbinding errors and informed guessing (Pratte, 2019). More specifically, in each trial, after 1 s delay, a white circle cueing the location of the probed orientation appeared for 200 ms, and participants were asked to report whether they remembered or forgot the probed orientation by pressing the left or right button of the mouse. The left–right buttons were counterbalanced across participants. Subsequently, participants were instructed to recall the targeted orientation at the

probed position within 4 s by moving the mouse and making a confirming click. Finally, participants rated their confidence in a seven-point scale (1, "lowest confidence"; 7, "highest confidence"), which was introduced as a validation of the remember–forget binary forced choice (Fig. 5A).

Participants completed six blocks of the delay estimation task before and after stimulation, each block included 60 trials, and each task lasted for ~20 min. In this experiment, we only focused on the high set size condition (i.e., Set Size 8) and included two tDCS sessions (i.e., PPC and sham). All stimulation setups were similar to Experiment 1 (Fig. 5*B*).

Data analysis

Replicate the overall tDCS effects on RT and nontarget response. Across all trials, we first examined tDCS effects over PPC on prolonged RT and increased pNT observed in Experiment 1 by conducting a two-way repeated–measure ANOVA for stimulation condition (PPC vs sham) and test time (pretest vs posttest). For significant two-way interaction effects, we further conducted simple effect tests. Similar to Experiment 1, for significant tDCS effects, we explored the potential influences of capacity and strategy through correlation analysis. Here, we used an advanced model fitting method to obtain all three parameters (pNT, pT, pU) for each trial (Schneegans and Bays, 2016).

Compare tDCS effects between remembered and forgotten trials. Trials were divided into remembered trials (trial number, M, 220.974; SD, 12.872) and forgotten trials (M, 131.371; SD, 10.570) based on the binary forced choice. Paired *t* tests revealed that errors for remembered trials were significantly lower than those for forgotten trials [M (SD), 16.280 (5.743) versus 29.208 (7.630); $t_{(28)} = -16.174$; p < 0.001; Cohen's d = -3.003; BF₁₀ > 1,000], and confidence ratings were also significantly higher for remembered trials than for forgotten trials [M (SD), 4.922 (0.960) versus 2.302(0.629); $t_{(28)} = 15.638$; p < 0.001; Cohen's d = 2.904; BF₁₀ > 1,000], suggesting that our metacognition categorization was validated, and forced choice self-reports reflected objective memory. Then, behavioral parameters for each trial type were averaged for follow-up tDCS effect comparisons.

For the tDCS effects on RT and *p*NT, we examined whether these effects differed across trial types through a three-way repeated–measure ANOVA of trial type (remembered vs forgotten), stimulation condition (PPC vs sham), and test time (pretest vs posttest). We further conducted two-way repeated–measure ANOVAs and simple effect tests for stimulation condition and test time in each trial type if the three-way interaction effects were significant. Other parameters were also tested in a similar way.

Experiment 3

Participants. Thirty-four healthy university students (18 females; M, 22.00 years; SD, 2.06) were recruited. Six participants were excluded due to poor performance, leaving 28 participants for the following analysis. The sample size choice, participant recruitment, and payment criteria were consistent with Experiment 2.

Experimental procedure. The change detection task for orientations was adapted from a previous study (Gong and Li, 2014; Fig. 6A). By including a lure-trial condition (Luck et al., 2009), we can examine the tDCS effects on the feature binding in VWM recognition. The encoding and maintenance periods were the same with the delayed estimation task, as well as the chosen orientation values. During the probe, a probed orientation appeared on the screen, and participants were required to make a judgment about whether the probed orientation changed compared with the orientation presented in the same location during the sample period, by pressing either the "F" or "J" key. The response keys were counterbalanced across participants, and the maximum response window was 2 s. The probabilities of orientation change and no change were equal. In the change trials, half of the probed orientation was different from all the orientations during the sample display, and it was 40° away from the target item (clockwise or anticlockwise) to make sure the change was detectable (i.e., "change trials"); the other half of the probed orientation was the same as the orientation located next to the probed location (i.e., "lure trials"). The change detection task consisted of 240 trials for each memory load (i.e., Set Size 6 and Set Size 8). Before and after stimulation, participants completed four blocks of the task, and each block consisted of 60 trials with two memory loads randomly mixed. The tDCS setup was consistent with Experiment 2 (Fig. 6*B*).

Code accessibility. For all three of experiments, data and code that support the findings are available on the Open Science Framework at https://osf.io/q84a2/. The code is available as Extended Data [noted that modeling was referred to previous work, please see Bays et al., (2009) and Schneegans and Bays (2016)].

Data analysis. Estimation of behavioral performance and tDCS effects. First, we calculated overall RT and accuracy under each memory load based on all trials. RT was defined as the duration between the onset of the probe and button-press response, and accuracy referred to the proportion of correctly response trials out of all trials. Then, we also obtain RT and accuracy in no change trials, lure trials, and change trials, respectively. In lure trials, higher accuracy indicated better feature binding ability and lower nontarget responses (e.g., lower *p*NT in Experiments 1 and 2). To examine the tDCS effects on each behavioral parameter, we performed a series of 2 (stimulated region, P4 vs sham) × 2 (test time, pre vs post) × 2 (memory load, Set Size 6 vs Set Size 8) ANOVAs. If their interactions were significant, we further analyzed tDCS effects on each memory load.

Besides, memory strategy scores were also collected in each set size. We replicated the results that the higher remembersubset strategy scores in Set Size 8 than that in Set Size 6 [SS6, M (SD), 3.250 (1.110); SS8, M (SD), 2.536 (1.071); difference, $t_{(27)}$ = 3.487; p = 0.0017; BF = 21.319], as well as the correlation between them (r = 0.5604; p = 0.0017; BF = 8.558). If significant tDCS effect was found, similar correlation analysis would be conducted. Based on the findings of Experiments 1 and 2, the effects of tDCS over PPC on overall RT and accuracy in lure trials were of most interest.

Results

Experiment 1

PPC stimulation prolonged recall RT

For tDCS effects over PPC in RT, the interaction effect of stimulation condition, test time, and memory load was not significant ($F_{(1,56)} = 0.595$; p = 0.444; $\eta_p^2 = 0.011$; BF₁₀ = 0.205), whereas the interaction between stimulation condition and test time was significant ($F_{(1,56)} = 6.228$; p = 0.016; $\eta_p^2 = 0.100$; BF₁₀ = 3.366). For both memory loads, we observed significant interactions between stimulation condition and test time (Fs > 5.179; ps < 0.027; $\eta_p^2 s > 0.085$; BF₁₀s > 2.309). Simple effect tests revealed that, although both PPC stimulation and sham stimulation lead to significantly reduced RT (ts > 5.406; ps < 0.001; Cohen's ds > 0.716; BFs₁₀ > 1,000), the decrease was smaller in tDCS over PPC compared with that in sham (i.e., a relatively longer RT after tDCS over PPC; Fig. 2*A*, left). Meanwhile, at the individual level, the tDCS effects on prolonged RTs between two memory loads were highly correlated ($r_{(55)} = 0.864$; p < 0.001; BF₁₀ > 1,000; Fig. 2*B*, top). Thus, we averaged RT changes in two memory loads to index the tDCS effects on RT in the following analysis. For tDCS effect over OCC in RT, on the contrary, our results revealed no three-way nor two-way interactions between test time and stimulation conditions (Fs < 2.622; ps > 0.111; $\eta_p^2 s < 0.045$; BF₁₀ < 0.458).

More importantly, we also found significant interactions between two stimulation conditions (i.e., PPC and OCC) and test time for both memory loads (Fs < 5.969; ps < 0.038; $\eta_p^2 s < 0.096$; $BF_{10}s < 4.908$). Similarly, further analyses found that the RT reduction was significantly smaller after PPC stimulation (Set Size 6, $t_{(56)} = 6.071$; p < 0.001; Cohen's d = 0.804; $BF_{10} > 1,000$; Set Size 8, $t_{(56)} = 5.406$; p < 0.001; Cohen's d = 0.716; $BF_{10} > 1,000$) than that after OCC stimulation (Set Size 6, $t_{(56)} = 8.179$; p < 0.001; Cohen's d = 1.083; $BF_{10} > 1,000$; Set Size 8, $t_{(56)} = 7.810$; p < 0.001; Cohen's d = 1.033; $BF_{10} > 1,000$). However, our results revealed that effect sizes of tDCS over PPC and OCC were not correlated across subjects ($r_{(55)} = 0.098$; p = 0.467; $BF_{10} = 0.214$; Fig. 2*B*, bottom). Together, these results indicated that PPC stimulation selectively prolonged RT.



Figure 2. *A*, Changes in RT and recall error across stimulation conditions and memory loads. The error bars represent standard error of the mean (SEM). Statistical test markers indicate significant stimulated region × test time interaction. **p* < 0.05. *B*, Correlation of tDCS effect over PPC across set sizes (top) and tDCS effect over regions (bottom).

Meanwhile, we did not find any significant interaction between test time and stimulation condition for tDCS effects on recall errors (*F*s < 2.202; *p*s > 0.143; η_p^2 s < 0.038; BF₁₀s < 0.218; Fig. 2A, right), suggesting no overall VWM performance changes after PPC or OCC stimulation.

PPC stimulation increased nontarget responses

For tDCS effects over PPC on *p*NT, we found significant interaction among stimulation condition, stimulation time, and memory load ($F_{(1,56)} = 10.226$; p = 0.002; $\eta_p^2 = 0.154$; BF₁₀ = 4.925). Follow-up two-way ANOVA showed that the interaction between the stimulated region and test time was only significant in Set Size 8 condition ($F_{(1,56)} = 7.593$; p = 0.008; $\eta_p^2 = 0.119$; BF₁₀ = 3.159; in Set Size 6, $F_{(1,56)} = 2.157$; p = 0.147; $\eta_p^2 = 0.037$; BF₁₀ = 0.473; Fig. 3*A*). For Set Size 8, nontarget responses were comparable before and after PPC stimulation ($t_{(56)} = 0.254$; p = 0.801; Cohen's d = 0.034; BF₁₀ = 0.149) but became significantly lower after sham stimulation ($t_{(56)} = 3.426$; p = 0.001; Cohen's d = 0.454; BF₁₀ = 24.009). Unlike the tDCS effects on RTs, the effect sizes of tDCS over PPC across memory loads were not correlated ($r_{(55)} = 0.062$; p = 0.646; BF₁₀ = 0.183; Fig. 3*B*, top).

To further examine the specificity of the tDCS effects of PPC on *p*NT, we compared *p*NT changes before and after stimulation over PPC and OCC in Set Size 8. The interaction between the stimulated region and test time was significant ($F_{(1,56)}$ =4.455; p=0.039; BF₁₀=2.319). Specifically, comparable *p*NTs were observed after PPC stimulation ($t_{(56)}$ =0.254; p=0.801; Cohen's d=0.034; BF₁₀=0.149), whereas decreased *p*NTs were found after OCC stimulation ($t_{(56)}$ =2.944; p=0.005; Cohen's d=0.390; BF₁₀=6.563). Similarly, there was no correlation between the tDCS effects over PPC and OCC on *p*NT ($r_{(55)}$ =-0.037; p=0.783; BF₁₀=0.172; Fig. 3*B*, bottom). Besides, additional correlation analysis revealed that tDCS effects on RT and *p*NT were also independent ($r_{(55)}$ =0.073; p=0.589; BF₁₀=0.191). Together, these results suggested that, compared with sham stimulation, PPC stimulation specifically increased nontarget responses in the high memory load.

Besides, for tDCS effects over PPC on precisions, target probability, and guessing probability, we only found a marginal three-way interaction effect among the stimulated region, test time, and memory load in *p*U ($F_{(1,56)}$ =3.244; *p*=0.077; η_p^2 =0.055; BF₁₀=1.542; others, *F*s < 2.732; *p*s > 0.104; η_p^2 s < 0.047; BF₁₀s < 0.159). Further analysis indicated that, in Set Size 8, PPC stimulation decreased the random guesses ($t_{(56)}$ =2.535; *p*=0.014; Cohen's *d*=0.336; BF₁₀=2.670) while no such difference in sham stimulation ($t_{(56)}$ =3.426; *p*=0.001; Cohen's *d*=0.454; BF₁₀=24.009). In contrast, neither three-way interactions nor two-way interactions were observed for OCC stimulation (*F*s < 2.862; *p*s > 0.434; BF₁₀s < 0.504), showing no tDCS effect over OCC on all fitting parameters. Together, our results suggested that tDCS over PPC specifically increased the nontarget response while decreasing the random guessing, without changing general VWM performance.



tDCS effects over PPC were not modulated by capacity or strategy

Correlation results showed that individual capacity or the recall strategy index were not correlated with the PPC tDCS effects of prolonged RT or increased pNT (rs < -0.213; ps > 0.112; BF₁₀s < 0.573; Fig. 4).

Figure 3. *A*, Changes in response precisions (κ), probability of target responses (pT), probability of nontarget responses (pNT), and probability of guessing (pU) across different stimulation conditions and memory loads. The error bars represent SEM. Statistical test markers indicate significant stimulated region × test time interaction. [#]0.05 < p < 0.1; *p < 0.05; **p < 0.01. *B*, Correlation of tDCS effect over PPC across set sizes (top) and tDCS effect over regions (bottom).



Figure 4. A, Correlation between memory capacity and tDCS effects. B, Correlation between memory strategy and tDCS effects. Note that effects on pNT were calculated under Set Size 8; effect on RT was averaged across two memory loads.

Summary of Experiment 1

Experiment 1 revealed that PPC stimulation specifically prolonged RT and increased *p*NT in the delayed estimation task, supporting the view that the parietal lobe played a critical role in content–context binding during VWM (Gosseries et al., 2018; Cai et al., 2020). In contrast, although studies reported OCC played an important role in information representation during VWM (Bettencourt and Xu, 2016), stimulation over the occipital lobe did not change VWM performance. The results suggested the higher brain areas may play a more causal role in VWM.

By introducing additional metacognition estimates, Pratte (2019) has proposed two types of nontarget responses: the misbinding trials where individuals reported high recall confidence (i.e., "remember trials"), and the informed guessing trials where individuals reported low confidence (i.e., "forgotten trials"). Researchers claimed that these two types of non-target responses reflected different cognitive and metacognitive processes (Huang, 2020; Mallett et al., 2022). Thus, in Experiment 2, we further examined whether PPC stimulation equally affected these two types of nontarget responses.

Experiment 2

PPC stimulation prolonged recall RT and increased nontarget responses

Consistent with Experiment 1, we observed a significant interaction between stimulation condition and test time on RT ($F_{(1,28)} = 5.894$; p = 0.028; $\eta_p^2 = 0.174$; BF₁₀ = 5.178). Post hoc tests revealed that the RT decrease after PPC stimulation ($t_{(28)} = 4.563$; p < 0.001; Cohen's d = 0.847; BF₁₀ = 282.944) was significantly smaller than that after sham stimulation ($t_{(28)} = 7.356$; Cohen's d = 1.366; p < 0.001; BF₁₀ > 1,000). For *p*NT, the interaction between stimulation condition and test time was also significant ($F_{(1,28)} = 4.498$; p = 0.045, $\eta_p^2 = 0.138$; BF₁₀ = 2.691). Post hoc analyses revealed that there was no difference after PPC stimulation ($t_{(28)} = 0.836$; p = 0.410; Cohen's d = 0.155; BF₁₀ = 0.272) but a significant decrease in *p*NT after sham stimulation ($t_{(28)} = 3.816$; p < 0.001; Cohen's d = 0.709; BF₁₀ = 46.613). Meanwhile, tDCS effects over PPC on RT and *p*NT were independent across participants ($r_{(27)} = -0.256$; p = 0.180; BF₁₀ = 0.544), and neither tDCS effect was correlated with individual differences in capacity or strategy [rs < -0.297; ps > 0.118; BF₁₀s < 0.739; capacity, M (SD), 5.497 (1.477); strategy score, M (SD), 3.455 (1.121)]. Besides, similar with the findings in Experiment 1, we observed a similar numerical trend of two-way interaction between stimulated region and test time for pU ($F_{(1,28)} = 2.780$; p = 0.107; $\eta_p^2 = 0.090$; BF₁₀ = 1.497), while there was no significant effects on recall error, confidence ratings, and other parameters (Fs < 0.978; ps > 0.331; $\eta_p^2 s < 0.034$; BF₁₀s < 0.403).

tDCS effects over PPC on RT were greater in forgotten trials than in remembered trials

We further examined the tDCS effects over PPC between forgotten and remembered trials. For RT, the interaction among trial type, stimulation condition, and test time were significant ($F_{(1,28)} = 6.385$; p = 0.017; $\eta_p^2 = 0.186$; $BF_{10} = 2.372$; Fig. 5*D*, top). Further two-way repeated–measure ANOVAs for each trial type indicated that the effect size in forgotten trials ($F_{(1,28)} = 11.506$; p = 0.002; $\eta_p^2 = 0.291$; $BF_{10} = 65.871$) was larger than in remembered trials ($F_{(1,28)} = 4.293$; p = 0.048; $\eta_p^2 = 0.133$; $BF_{10} = 2.244$). For *p*NT, however, no significant interaction effect among trial type, stimulation condition, and test time were observed (Fs < 2.707; ps > 0.111; $\eta_p^2 < 0.088$; $BF_{10} < 0.225$; Fig. 5*D*, bottom), indicating comparable tDCS effects in two types of nontarget trials.

Summary of Experiment 2

In Experiment 2, we replicated the main findings of Experiment 1 that PPC stimulation increased RT and *p*NT during VWM. More importantly, compared with remembered trials, tDCS effects on RT were greater in forgotten trials while were comparable on *p*NT. In sum, these results suggested that PPC was causally involved in two types of nontarget responses, while it may be through different mechanisms.



Figure 5. *A*, Schematic diagrams of the delay estimation task. *B*, tDCS procedures. *C*, Changes in RT, error, confidence rating, and fitting parameters across stimulation conditions. The error bars represent SEM. Statistical test markers indicate significant interactions. *0.05 ; <math>*p < 0.05; *p < 0.01. *D*, Changes in RT and *p*NT for remembered and forgotten trials across stimulation conditions.

A recent computational modeling study indicated that VWM recall and recognition involved different cognitive processes (Kahana, 2020). Since delayed estimation and change detection are two typical VWM tasks to estimate memory recall and recognition respectively, we further examined whether the tDCS over PPC mainly affected VWM retrieval processes and caused behavioral changes, by using a change detection task in Experiment 3.

Experiment 3

No tDCS effect over PPC on RT or misbinding processes in recognition

No interaction effect between stimulation and test time was significant for RT (Fs < 1.251; ps > 0.273; $\eta_p s^2 < 0.044$; $BF_{10}s < 0.390$) or for accuracy in lure trials (Fs < 0.832; ps > 0.370; $BF_{10}s < 0.391$), indicating that PPC stimulation did not affect RT or binding processes in VWM recognition (Fig. 6*C*,*D*). Similarly, there was no significant interaction effect on other behavioral parameters (Fs < 1.235; ps > 0.246; $\eta_p s^2 < 0.042$; $BF_{10}s < 0.586$; except for a trend effect on accuracy in high memory load in no change trials, $F_{(1,27)} = 3.441$; p = 0.075; $BF_{10} = 0.945$).

Discussion

The current study established the causal relationship between posterior parietal activity and feature binding during VWM retrieval through three tDCS experiments. First, we found that anodal tDCS over PPC selectively increased recall RT as well as nontarget responses in the delayed estimation task. Meanwhile, combined with metacognitive evaluations, we clarified these tDCS effects could be observed in both types of nontarget responses (i.e., misbinding and informed



Figure 6. A, Schematic diagrams of the change detection task. B, tDCS procedures. Changes in RT (C) and accuracy (D) across trial types and stimulation conditions. The error bars represent SEM.

guessing). Besides, we further identified that the effects of tDCS over PPC were specific during memory retrieval by demonstrating that such effects were not observed during memory recognition. Together, our findings deepen our understanding of the involvement of PPC in the feature binding during VWM retrieval.

First of all, in two independent samples, we replicated that anodal tDCS over PPC increased nontarget responses in the delayed estimation task. These results supported recent fMRI studies that emphasized the close relationship between posterior parietal activity and the feature binding processes during VWM (Gosseries et al., 2018; Cai et al., 2020). Meanwhile, we noticed the increased nontarget responses along with a trend of decreased random guesses. That is, tDCS over PPC biased the recall process. Two possibilities could explain these findings. One possibility is that enhanced posterior parietal activity may facilitate the reinstatement of content information from multiple items during retrieval, leading to an increased probability of nontarget responses. Supporting this view, Baddeley (2000) proposed the posterior parietal lobe as a core area for the episodic buffer during WM, and Xie et al. (2017) further interpreted PPC as a hub of multisensory information integration, which claimed PPC's critical role in representing and combining different features. Moreover, our results emphasized that PPC was causally involved during memory retrieval instead of recognition. Comparing the delayed estimation and change detection tasks, previous studies have shown similar neural activity during WM maintenance. For instance, EEG studies have found similar contralateral delay activity (Vogel and Machizawa, 2004; Adam et al., 2018; Cai et al., 2022), and fMRI studies showed similar frontoparietal activity during these two tasks (Cai et al., 2018; Kim, 2019). In contrast, during the response, a recent study suggested that the delayed estimation task is mainly based on detailed retrieval while the change detection task is based on familiarity judgment (Kahana, 2020). Although few studies directly compared the PPC activity between recall and recognition during WM, considerable evidence has supported the critical role of PPC in episodic memory retrieval but not in recognition. For example, studies have revealed that both activation strength (Wagner et al., 2005; Cabeza et al., 2008; Sestieri et al., 2017) and the neural representations in PPC (Xiao et al., 2017) increased during memory retrieval but not during recognition (Dobbins et al., 2003). Currently, our findings confirmed the causal relationship between the PPC and retrieval during VWM, which was similar to those in episodic memory.

Another possibility proposed that enhanced posterior parietal activity may increase cognitive resources and lead to the adoption of a more proactive retrieval strategy, increasing nontarget responses. Our results revealed that tDCS over PPC comparably increased both types of nontarget responses (i.e., misbinding and informed guessing). Researchers have proposed that misbinding responses were generated when participants misorganized information across different items, while informed guessing reflected participants actively making choices from all the memorized information (Pratte, 2019). Consistently, recent studies revealed that misbinding mainly resulted from less efficient information processing during early encoding or storage (Emrich and Ferber, 2012; Zokaei et al., 2014; Pertzov et al., 2017) whereas informed

guessing more likely reflected the different neural activity during late storage or memory retrieval (Pratte, 2019; Huang, 2020). Consequently, both nontarget responses required more cognitive effort compared with random guesses. From the source-consumption perspective, the latest study revealed that parietal tDCS could reduce the cumulative fatigue effect during tasks (Hemmerich et al., 2023). Therefore, we could not exclude the possibility that anodal PPC stimulation enabled individuals to generate both more proactive nontarget responses during VWM retrieval.

Besides, we also found that PPC stimulation prolonged recall RT, which was in line with both explanations about increased nontarget responses above. However, some evidence in the current study suggested that the tDCS over PPC affected recall RT and feature binding through different pathways. For example, we found that tDCS over PPC only increased nontarget responses under high memory load, whereas it changed RTs across memory loads, and the effects were highly correlated across loads at the individual level. Meanwhile, we observed greater tDCS effects on RTs in informed guessing trials than in misbinding trials, while comparable effects on nontarget responses between these two types of trials. Furthermore, tDCS effects on RTs and nontarget responses were always independent at the individual level. Supporting these findings, the latest meta-analysis demonstrated that different PPC stimulation patterns enhanced WM accuracy and RT separately (i.e., different frequencies; Wischnewski et al., 2024). However, future studies are needed to further clarify how PPC is differently involved in the recall speed and accuracy of memory retrieval.

To be noted, our findings were not consistent with some previous relevant studies. Regarding the tDCS effects on increasing the nontarget response during the delayed estimation task, for example, using a similar paradigm, another study found anodal PPC stimulation did not change the nontarget response rate but increased the recall precision. On the opposite, the PPC cathodal stimulation decreased the nontarget response rate and increased the target response rate and recall precision (Heinen et al., 2016). In this study, the reversed tDCS effect of cathodal stimulation on the nontarget response rate could be well explained by the polarity effects of tDCS reported in accumulating studies (Nitsche and Paulus, 2000; Stagg and Nitsche, 2011) and supported the causality between PPC activities and feature bindings observed in the current study. Meanwhile, we would attribute the inconsistent anodal stimulation effects across studies to differences in timings of stimulations as well as task difficulty. The tDCS in our study was conducted when participants took a rest between tasks while the stimulation in Heinen's study was conducted exactly during the tasks. According to the recent state-dependent theory, the neural modulation effects were largely dependent on the ongoing neural states (Bradley et al., 2022). Besides, the tDCS effects in our study were observed in a supra-capacity condition (Set Size 8), while tDCS effects in Heinen's study were in a much lower, around-capacity condition (Set Size 4). According to previous studies, task difficulty could be a critical modulation factor influencing the tDCS effects (Pope and Miall, 2012; Vergallito et al., 2022). Given that participants were more likely to employ the remember-subset strategy in the high-load condition, it is plausible that tDCS may have specifically impacted cognitive processes underlying this memory strategy (e.g. suppression "distractors" beyond memory capacity). In addition, we did not find that tDCS over PPC improved the general VWM performance in either delayed estimation or change detection tasks, which was consistent with some recent studies (Heinen et al., 2016; Robison et al., 2017; Jiang et al., 2024) but challenged some other earlier studies (Li et al., 2017; Wang et al., 2019). Besides, we did not replicate the correlation between tDCS effects and individual capacity (Tseng et al., 2012; Hsu et al., 2014) or the adoption of remember-subset strategy (Wang et al., 2020). Usually, as we mentioned above, researchers suggested that these differences could be generally explained by a series of detailed methodological settings. However, regarding our null tDCS effects in the change detection task, in particular, we also suggested to understand these differences from the different probed displays and stimulus type. For example, Tseng et al. (2012) used a change detection task with the whole-item comparison design while we used the singleitem comparison. Previous studies have revealed that the change detection judgments on the whole-item display can depend on additional integrated information (such as the general configuration and relationships between items) while singleitem judgment cannot (Morey, 2011; Rouder et al., 2011). Thus, the tDCS over PPC may only facilitate processes for more integrated information instead of single-item retrieval. Meanwhile, we cannot exclude the differences was caused by varying stimuli across studies given there are not a few studies have revealed dissociated cognitive and neural basis underlying VWMs for different stimulus types (e.g., color vs orientation; Jackson et al., 2011; Huang, 2015).

Different from the PPC stimulation effects, it is noteworthy that we did not observe any tDCS effects over the occipital cortex on VWM. A set of recent studies found there was a location-specific neural representation in the occipital cortex which requires accurate item–context binding (Fulvio et al., 2023; Teng and Postle, 2024), and some other studies also reported these neural representations predicted nontarget responses at the individual level (van Lamsweerde and Johnson, 2015; Cai et al., 2020). We suggested two possible explanations for this inconsistency. First, unlike the sustained activation of PPC during maintenance, the neural representations of the item or its context information did not depend on sustained activation in the occipital cortex (Harrison and Tong, 2009; Riggall and Postle, 2012). Since tDCS is expected to increase the neural activity of specific areas instead of promoting the neural representation directly, tDCS over the occipital cortex could not significantly affect behavior. Second, previous studies have suggested that occipital neural activity is regulated by feedback signals from the frontal and posterior parietal regions (Halgren et al., 2002). Therefore, even if the occipital neural representation is affected by tDCS, the occipital cortex could maintain the memory information efficiently by receiving feedback signals from other brain areas. Together, these results indicated that the occipital activity has no causal effect on VWM performance or feature binding process.

Finally, some limitations need to be paid attention in the current study. First, our results were not consistent with some relevant studies mentioned above, and we cannot identify whether these differences are attributed to some specific

factors (i.e., task paradigm, difficulty, stimulus type, individual differences, timing of stimulation, etc.) or a more complex interaction effect between them. Although our findings may not end the existing controversies, our study strongly reminded that future studies should systematically explore the potential factors influencing tDCS effects, and combining the high-definition stimulations and neuroimaging methods could provide insightful views. Second, we found that single-session tDCS only changed the response bias for nontargets but failed to change overall working memory performance, which should be further explored in future studies. For example, recent studies have demonstrated that local brain oscillations and interarea synchronizations contributed to feature binding during VWM (Barbosa et al., 2019; Zhang et al., 2019); thus future studies using transcranial alternative current stimulation (tACS) to change these band-specific neural activities may better improve the binding efficiency and VWM performance. Meanwhile, recent studies have also demonstrated that high-frequency randomized noise stimulation reveals a stronger effect on changing the cortical activities, which could also be a potential way to improve the general VWM performance (Terney et al., 2008; Murphy et al., 2020).

In conclusion, the present study demonstrates that enhanced posterior parietal activity prolongs RT in VWM retrieval and increases the probability of binding errors, and these effects are observed in two types of binding errors (i.e., misbinding and informed guessing). Our findings provide direct evidence of the causal relationship between the PPC and feature binding, deepening our understanding of the neural basis of feature binding in VWM.

Data and code availability statement

Data and code that support the findings of this study are available on the Open Science Framework at https://osf.io/q84a2/.

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