

Dissociated roles of the parietal and frontal cortices in the scope and control of attention during visual working memory

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ARTICLE INFO

Keywords:

Visual WM
Attention scope
Attention control
PPC
PFC
tDCS

ABSTRACT

Mounting evidence suggests that multiple mechanisms underlie working memory capacity. Using transcranial direct current stimulation (tDCS), the current study aimed to provide causal evidence for the neural dissociation of two mechanisms underlying visual working memory (WM) capacity, namely, the scope and control of attention. A change detection task with distractors was used, where a number of colored bars (i.e., two red bars, four red bars, or two red plus two blue bars) were presented on both sides (Experiment 1) or the center (Experiment 2) of the screen for 100ms, and participants were instructed to remember the red bars and to ignore the blue bars (in both Experiments), as well as to ignore the stimuli on the un-cued side (Experiment 1 only). In both experiments, participants finished three sessions of the task after 15 min of 1.5 mA anodal tDCS administered on the right prefrontal cortex (PFC), the right posterior parietal cortex (PPC), and the primary visual cortex (VC), respectively. The VC stimulation served as an active control condition. We found that compared to stimulation on the VC, stimulation on the right PPC specifically increased the visual WM capacity under the no-distractor condition (i.e., 4 red bars), whereas stimulation on the right PFC specifically increased the visual WM capacity under the distractor condition (i.e., 2 red bars plus 2 blue bars). These results suggest that the PPC and PFC are involved in the scope and control of attention, respectively. We further showed that compared to central presentation of the stimuli (Experiment 2), bilateral presentation of the stimuli (on both sides of the fixation in Experiment 1) led to an additional demand for attention control. Our results emphasize the dissociated roles of the frontal and parietal lobes in visual WM capacity, and provide a deeper understanding of the neural mechanisms of WM.

Introduction

It is well established that working memory (WM) capacity is limited and only a small amount of information can be temporally maintained in the focus of attention. Existing studies have suggested that WM capacity is determined by multiple cognitive processes (Baddeley, 2003; Cowan et al., 2005; Cowan et al., 2006; D'Esposito and Postle, 2015; Kane and Engle, 2002). In the classic storage-and-processing model of WM (Baddeley, 2003; Baddeley and Logie, 1999; Baddeley, 1986), which was built upon earlier work that emphasized short-term storage (Miller, 1956) and controlled processes (Atkinson and Shiffrin, 1968), a “visuospatial sketchpad” and a “phonological loop” store visual and verbal information, respectively, and are under the control of the united “central executive” (Baddeley, 1992; Baddeley and Hitch, 1974).

In a more recent model of WM, Cowan and colleagues dissociated

two attention components, i.e., the scope and the control of attention, that contribute to WM performance. The scope of attention measures the amount of information people can maintain in WM at a given point in time, whereas the control of attention refers to the ability to actively direct attention to goal-relevant information, and away from goal-irrelevant information (Cowan et al., 2005; Cowan et al., 2006). The scope of attention is a capacity-limited process that plays a major, but not exclusive, role in determining WM capacity, because the latter is determined by multiple cognitive processes, including the scope and control of attention. The role of attention control in WM is also emphasized in the attention-control view of WM proposed by Engle and colleagues (Kane et al., 2001; Kane and Engle, 2002). According to this view, the control of attention shares many critical processes with selective attention. Consistently, studies have found that larger WM capacity results from better attention control by filtering out irrelevant

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information (Conway et al., 2001; Vogel et al., 2005), overriding attentional capture by distractors (Fukuda and Vogel, 2009; Kane et al., 2001), and suppressing salient distractors (Gaspar et al., 2016).

Behavioral studies have further suggested that the scope and the control of attention are dissociated and make independent contributions to WM performance. For example, a developmental study found that children had limited attention control ability and only their scope of attention was correlated with intelligence, but for adults, both the scope and control of attention distinctly contributed to intelligence (Cowan et al., 2006). Another study found that multimedia multitaskers showed specific impairment in attention control (termed information filtering) but not in attention scope (Ophir et al., 2009). Using structural equation modeling on a variety of WM tasks, two recent studies found that the scope and control of attention were independent components of WM (Shipstead et al., 2014; Shipstead et al., 2012).

At the neural level, both the prefrontal and parietal lobules have been implicated in attention scope (Eriksson et al., 2015) and attention control (Corbetta and Shulman, 2002). Of greater relevance to the current study, however, these two regions have also shown a certain level of functional dissociation. For example, lesion studies suggest that certain types of frontal lobe damage impair the control of attention, whereas certain types of parietal lobe damage change the attention scope (Cowan, 1995). Consistent with the lesion studies, fMRI studies have also documented associations between the PFC and attention control (Kane and Engle, 2002; Knight et al., 1995) and between the parietal cortex and attention scope (Chun and Johnson, 2011). Specifically, the PFC as well as the basal ganglia is believed to control the access to WM and the selection of relevant information stored in the parietal lobule (McNab and Klingberg, 2008). It was found that a lesion to the PFC impaired monkeys' ability to use cues to guide their attention, making them more easily distracted by visual stimuli associated with a response (Gregoriou et al., 2014). In contrast, the parietal cortex has been linked to attention scope. For example, the strength of BOLD response (Cowan et al., 2011; Kawasaki et al., 2008; Todd and Marois, 2004, 2005; Xu and Chun, 2006) and the amplitude of EEG's contralateral delay activity (CDA) (McCollough et al., 2007; Vogel and Machizawa, 2004) in the parietal lobule tracked attention scope or the number of items maintained in WM. Stimulation of the parietal lobule using either transcranial magnetic stimulation (TMS) (Sauseng et al., 2009) or transcranial direct current stimulation (tDCS) (Berryhill et al., 2010; Heimrath et al., 2012; Hsu et al., 2011; Jones and Berryhill, 2012; Tseng et al., 2012) affects attention scope.

The above studies examined separately the roles of the PFC and PPC in WM. There are also studies that have directly examined their dissociation (Buschman and Miller, 2007; Linden et al., 2003). For example, the PPC showed a sustained activation and feature selectivity during the whole delay period, whereas the PFC subregions showed only feature selectivity or sustained activation in a visual WM task when distractors were presented, suggesting that the frontoparietal subregions might play distinctive roles in top-down control and the maintenance of task-relevant information (Ester et al., 2015). Using a visual WM task, Tanoue et al. (2013) found that cathodal tDCS to the PFC had a significantly stronger effect than did stimulation to the PPC in the retro-cuing condition. This finding corroborated an earlier fMRI study (Lepsien and Nobre, 2006) suggesting that the PFC is involved in shifting attention to internal representation under the retro-cuing condition. Finally, two studies used rTMS to examine the roles of the frontal and parietal lobules in spatial working memory and found a functional dissociation of the two regions. One study found that only DLPFC stimulation affected performance (Hamidi et al., 2009), whereas the other study found that PPC but not DLPFC stimulation reduced task performance (Pearce et al., 2014).

To summarize, although it has been suggested the PFC and PPC might be involved in different processes that affect visual WM capacity, few studies have examined the differential (causal) roles of the frontal

and parietal lobules in the scope and control of attention when performing visual WM tasks. The few studies that have been conducted focused only the effect for one brain region and/or one task. There is still a lack of direct evidence that these two regions show a functional dissociation for attention scope and control. The present study aimed at examining this issue with tDCS. A distractor version of the change detection task (Vogel et al., 2005) was used to measure attention scope (when distractors were not presented) and attention control (when distractors were presented). Because existing studies found that the right hemisphere was more closely associated with visual WM than was the left hemisphere (Habekost and Rostrup, 2007), we selected the right PPC (Berryhill and Jones, 2012; Tseng et al., 2012) and PFC (Wu et al., 2014) as the target regions. The visual cortex was chosen as the control region. Anodal stimulation was used because both animal (Bikson et al., 2004) and human models (Liebetanz et al., 2002; Nitsche et al., 2003) suggest that anodal tDCS increases the excitability of the stimulated cortical regions (Hsu et al., 2014; Keeser et al., 2011; Meinzer et al., 2012; Tseng et al., 2012). We predicted that, compared to stimulation on the visual cortex, anodal stimulation on the PPC would increase the scope of attention and thus the performance in the no distractor condition, whereas stimulation on the PFC would facilitate attention control and thus performance in the distractor condition.

Experiment 1

Methods

Participants

Twenty-seven (15 females; 22.15 ± 2.2 years old) neurologically healthy college students were recruited. Two additional subjects were recruited but whose data were excluded from analysis due to their chance-level performance (accuracy < 51%) after visual cortex (VC) stimulation. All participants had normal or corrected-to-normal vision and gave informed consent prior to their participation. The experimental procedures were approved by the Institutional Review Board of the State Key Laboratory of Cognitive Neuroscience and Learning at Beijing Normal University.

Experimental task

The stimuli were similar to a previous study (Vogel et al., 2005, Experiment 1) except that the orientation of the bars in our study were randomly selected from 0° to 360° (Fig. 1A) rather than a fixed set of four orientations (vertical, horizontal, left 45° , and right 45°).

A change detection task was used in the experiment (Fig. 1B). In each trial, a centrally placed cross fixation with an arrow cue above it directing to the left or right were presented for 200 ms, followed by two arrays of red or blue bars presented on the left and right sides of the screen for 100 ms. Participants were instructed to remember the red bars (targets) and to ignore the blue bars (distractors) on the cued side. The bar array included either two red bars (i.e., the “2 targets” condition), four red bars (i.e., the “4 targets” condition), or two red plus two blue bars (i.e., the “2 targets + 2 distractors” condition). After a blank interval of 900 ms, a test array was presented on both sides of the screen, and participants were required to judge whether the orientations of red bars on the cued side were changed. In 50% of the trials for each condition, one of the red bars on the cued side was rotated by 45 degrees. To make sure that subjects were responding according to the bars on the cued side, one of the red bars on the un-cued side also changed on 50% of the trials. The blue distractors were never changed. Participants made their responses by pressing corresponding buttons on the RT Box (Li et al., 2010) with their left or right index finger. The buttons for yes/no responses were counterbalanced across participants.

The behavioral task was programmed with Psychtoolbox 3 (<http://psychtoolbox.org>) and administered on an IBM-compatible computer. The screen resolution was set to 1024×768 and vertical refreshing rate

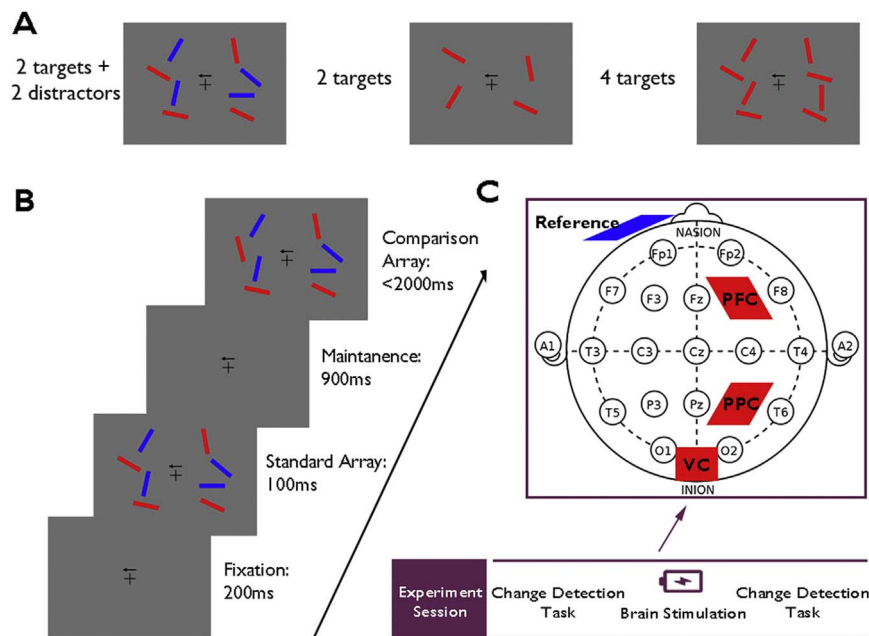


Fig. 1. Experimental design and the tDCS protocol. (A) The stimuli used in Experiment 1. (B) Trial structure. Each trial started with an arrow above fixation indicating the visual field to which participants should attend. Then two sets of bars were presented simultaneously on both sides of the screen. After a blank screen of interval, comparison arrays were presented, and participants needed to judge whether one of the red bars in the target visual field was rotated. (C) tDCS stimulations (red) were conducted on the right PFC, right PPC, and VC, according to the 10–20 electronic system. The reference was placed on the left cheek (blue). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

was 60 Hz. Participants were comfortably seated approximately 100 cm away from the computer screen in a soundproof, light-adjustable room. They were also instructed to fixate on the center of the screen throughout the study while holding their body still.

tDCS procedure

Participants completed three sessions of the task that were separated by 48 h between sessions, with anodal stimulation on the right prefrontal cortex (PFC), the right posterior parietal cortex (PPC), and the primary visual cortex (VC), respectively (Fig. 1C). The VC stimulation served as an active control condition. The order of the stimulation sessions was counterbalanced across participants. For each session, participants completed 3 runs of 180 trials (60 trials per condition) both before and after the stimulation (see below). There was a short break (3–5 min) between runs.

tDCS was delivered with a NeuroConn-DC-Stimulator by a pair of electrodes housed in 5×5 cm saline solution-soaked sponge coverings. The locations of the tDCS were determined by the international 10–20 EEG electrode placement system. For there was no clear evidence to show a strong lateralization effect on visual WM in tDCS studies, we followed the previous studies that used similar tasks or imaginary stimuli (Courtney et al., 1998) and selected the PFC and PPC in the right hemisphere for stimulation. The right PFC was located in F4 (Berryhill and Jones, 2012; Wu et al., 2014), the right PPC in P4 (Hsu et al., 2014; Tseng et al., 2012), and the VC in Oz (Lu et al., 2015; Xue et al., 2012). The reference electrode was placed on the left cheek (Tseng et al., 2012; Xue et al., 2012) (Fig. 1C). During brain stimulation, a direct current of 1.5 mA (0.06 mA/cm²) was applied for 15 min. The maximum total charge in the current experiment was 0.054 C/cm². Both the direct current and the total charge were lower than the safety criteria of 25 mA/cm² for densities and 216 C/cm² for total charge (Nitsche et al., 2003). Additionally, a 15 s fade-in and fade-out design was added before and after stimulation to reduce the sensation caused by tDCS.

Behavior data analysis

The task performances were estimated by Cowan's K (Cowan, 2001;

Cowan et al., 2005; Pashler, 1988), which uses hit rate and false alarm rate to estimate the number of to-be-remembered items or targets that are retained in working memory. The formula is $K=S*(H-F)$, where K is the number of targets in memory, S the size of the array, H the observed hit rate, and F the false alarm rate. The capacity for the "2 targets" condition for all participants before stimulation was close to 2 (capacity: 1.930 ± 0.525 items, $t(26)=-0.692$, $p=0.495$), which suggested a ceiling effect for the "2 targets" condition. As a result, the score for attention scope was calculated by the K under the "4 targets" condition. In contrast, the score for attention control was calculated by the differences between the K under the "2 targets + 2 distractors" condition and the K under the "2 targets" condition, using the following formula: Attention control score = $2+K$ (the "2 targets + 2 distractors" condition) – K (the "2 targets" condition). A higher score indicated better attention control.

The tDCS effect was measured as the difference between pre- and post-stimulation performance. We used two-way repeated-measures ANOVA with site (right PFC vs. PPC vs. VC) and attention component (scope vs. control) as within-subject measures to investigate the condition-by-site interaction. To examine performance-dependent tDCS effects, we divided the participants into high- and low-performance groups based on their attention scope and attention control scores separately, using median scores as the cut-off values. A mixed-effect three-way ANOVA was used to examine the tDCS effect with performance group as a between-subject factor, and site (right PFC vs. PPC vs. VC) and attention component (control vs. scope) as within-subject factors. Post-hoc tests were done using paired-sample t-test with Bonferroni correction for multiple comparisons.

Results

Pre-stimulation performances

A condition ("2 targets + 2 distractors" vs. "2 targets" vs. "4 targets") by stimulation site (right PFC vs. PPC vs. VC) ANOVA on the pre-stimulation performances (Cowan's K) revealed no effect of stimulation site ($F(2, 52) < 1$, $p=0.913$), or condition-by-stimulation-

Table 1
Reaction times (Standard Deviation in parentheses) for Experiments 1 and 2.

		2 targets+2 distractors	2 targets	4 targets
PPC	EXP1 Pre	0.677 (0.152)	0.656 (0.157)	0.717 (0.166)
	EXP1 Post	0.593 (0.139)	0.570 (0.131)	0.622 (0.140)
	EXP2 Post	0.581 (0.090)	0.555 (0.084)	0.600 (0.083)
PFC	EXP1 Pre	0.675 (0.142)	0.644 (0.137)	0.694 (0.145)
	EXP1 Post	0.601 (0.139)	0.580 (0.139)	0.620 (0.141)
	EXP2 Post	0.540 (0.116)	0.514 (0.105)	0.560 (0.110)
VC	EXP1 Pre	0.665 (0.174)	0.639 (0.166)	0.687 (0.180)
	EXP1 Post	0.596 (0.141)	0.568 (0.133)	0.623 (0.162)
	EXP2 Post	0.562 (0.113)	0.540 (0.110)	0.580 (0.119)

site interaction ($F(4,104)=0.537, p=0.709$), suggesting that there were no systematic biases in general cognitive states across the three experiment days. A similar ANOVA on RT also revealed no effect of stimulation site ($F(2, 52)=0.230, p=0.795$), or condition-by-stimulation-site interaction ($F(4,104)=1.818, p=0.131$) (Table 1).

Correlations between measures

There was a significant positive correlation between the scores of attention control and attention scope before stimulation ($r=0.414, p=0.032$) (Fig. 2A). The correlation was also significant after the stimulation on the right VC, ($r=0.611, p < 0.001$) (Fig. 2D), but not after the stimulation on the right PPC ($r=0.200, p=0.319$) or right PFC ($r=-0.231, p=0.246$) (Fig. 2B C).

tDCS effect on visual WM attention scope and attention control

The effect of tDCS was measured by the difference between pre- and post-stimulation performance (Table 2). A two-way repeated measures ANOVA on tDCS effects with site (right PFC vs. PPC vs. VC) and attention component (control vs. scope) as within-subject measures showed a significant interaction between stimulation site and attention component ($F(2, 52)=9.714, p < 0.001$). One-way ANOVA on the change of attention scope showed a significant main effect of stimulation site ($F(2, 52)=8.455, p < 0.001$). Post hoc paired-t tests showed that, compared to VC stimulation, stimulation on the right PPC

Table 2
tDCS Effect (Standard Deviation in parentheses) for Experiments 1 and 2.

		Attention Control	Attention Scope
PPC	EXP1 Pre	1.922 (0.161)	1.884 (0.726)
	EXP1 Post	1.822 (0.217)	2.398 (0.753)
	EXP2 Post	1.825 (0.151)	3.135 (0.381)
PFC	EXP1 Pre	1.826 (0.204)	1.858 (0.679)
	EXP1 Post	1.973 (0.158)	2.094 (0.604)
	EXP2 Post	1.953 (0.229)	2.781 (0.441)
VC	EXP1 Pre	1.868 (0.174)	1.909 (0.666)
	EXP1 Post	1.884 (0.165)	1.897 (0.751)
	EXP2 Post	1.862 (0.149)	2.679 (0.418)

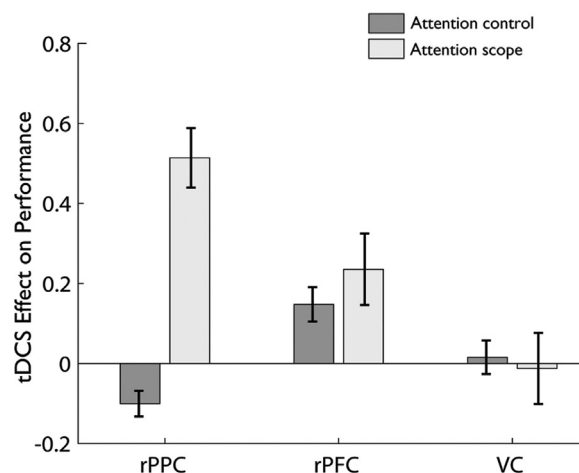


Fig. 3. tDCS effects in Experiment 1. The tDCS effects on attention control and attention scope (calculated as the difference between post- and pre-stimulation performance) are plotted as a function of experiment condition and stimulation site. Error bars denote standard errors of the mean (SEM).

significantly enhanced attention scope ($t(26)=4.069, p=0.001$), and the effect of PFC stimulation was marginally significant ($t(26)=2.039, p=0.052$) (Fig. 3). The effect of PPC stimulation was marginally greater than that of PFC stimulation ($t(26)=2.094, p=0.092$). For attention

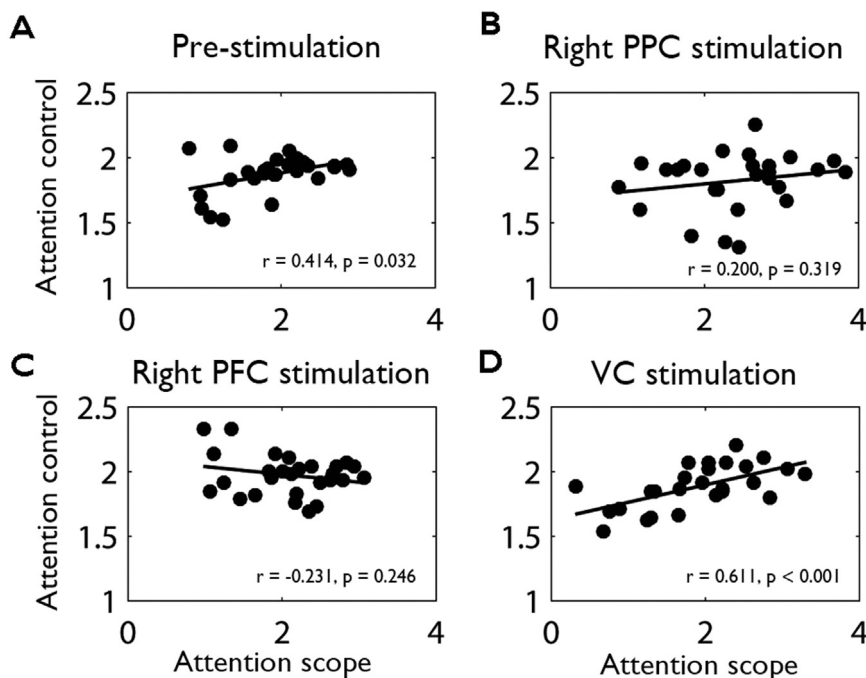


Fig. 2. Correlation of attention scope and attention control before stimulation (A) and after PPC (B), PFC (C), and VC stimulation (D) in Experiment 1.

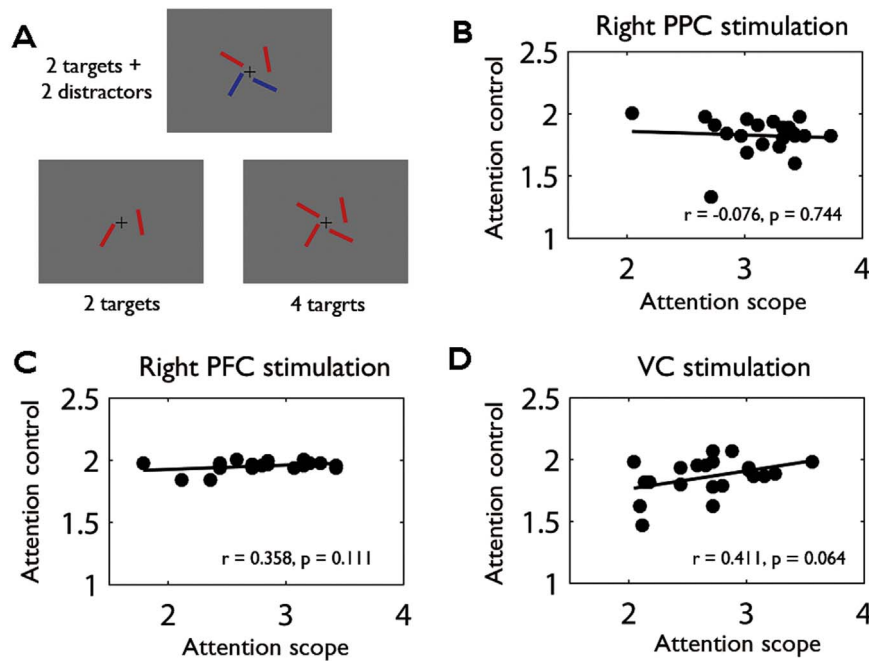


Fig. 4. The stimuli and results in Experiment 2. (A) Red bars were targets and blue ones were distractors. Only one set of bar arrays was presented on the center of the screen. (B–D) Correlations between attention scope and attention control indices in Experiment 2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

control, there was a significant main effect of stimulation site ($F(2, 52) = 9.075, p = 0.004$). Post hoc paired- t tests showed that, compared to VC stimulation, stimulation on the right PFC significantly enhanced the performance ($t(26) = 2.433, p = 0.044$), but stimulation on the right PPC showed an opposite trend ($t(26) = -1.871, p = 0.073$), yielding a significant difference between the sites of stimulation ($t(26) = 4.254, p < 0.001$) (Fig. 3).

Performance-dependent tDCS effect

Recent studies have suggested a performance-dependent tDCS effect, with generally stronger effects for participants with poorer task performance (Liang et al., 2014; Tseng et al., 2012). To examine this effect with respect to attention scope, we divided participants into two groups based on their averaged K values under the “4 targets” condition before stimulation ($n = 14$ and $n = 13$ for low- and high-performance groups, respectively). A two-way ANOVA on changes in attention scope between pre- and post-stimulation on right PPC showed no significant interaction between stimulation site and performance group ($F(1, 25) < 1, p = 0.917$), suggesting a lack of performance-dependent effect of right PPC stimulation on attention scope. Additional analyses involving PFC and VC stimulation also showed no performance-dependent effects (details omitted because of our focus on the role of the PPC in attention scope).

Similarly, to examine the performance-dependent effect with respect to attention control, we divided participants into two groups based on their averaged attention control score before stimulation ($n = 14$ and $n = 13$ for low- and high-performance groups, respectively). A similar two-way ANOVA on changes of attention control between pre- and post-stimulation on right PFC showed no significant interaction between stimulation site and performance group ($F(1, 25) = 1.833, p = 0.188$), suggesting a similar tDCS effect for both groups. Additional analyses involving PPC and VC stimulation also showed no performance-dependent effects (details omitted because of our focus on the role of the PFC in attention control).

Experiment 1: Summary

To summarize, Experiment 1 showed that consistent with our hypothesis, anodal tDCS on the right PPC enlarged visual WM attention scope, whereas anodal tDCS on the right PFC facilitated attention control. Interestingly, tDCS on the right PFC was also associated with improved attention scope, although this effect was not as significant as that of right PPC stimulation. This effect could be due to two possibilities. One possibility is that the PFC may be involved in both attention control and attention scope in visual WM. Alternatively, the bilateral presentation of stimuli (i.e., sets of bars on both sides of the fixation) used in this study required the participants to ignore one side of the screen. This was likely to impose a strong demand for attention control even under the distractor-free condition (Sauseng et al., 2009). This additional demand for attention control may also account for the significant correlations between attention control and scope before stimulation and after VC stimulation. In other words, the attention scope calculated using the “4 targets” condition may reflect both attention scope and attention control under the bilateral presentation paradigm.

To further examine these possibilities, we conducted Experiment 2 where a single array of stimuli was presented in the center of the screen. Given that no distractors were presented, this task could be considered as a purer measure of attention scope in visual WM (Fukuda et al., 2015). With a lower demand for attention control, we predicted a clearer dissociation of attention control and attention scope. Specifically, we predicted that (1) compared to bilateral presentation, central presentation would increase memory performance; (2) there would be no significant correlation between the two indices of visual WM (scope and control); and (3) right PPC stimulation would specifically enhance attention scope, whereas right PFC stimulation would specifically enhance attention control.

Experiment 2

Methods

Twenty-one (13 females; 21.24 ± 1.9 years old) neurologically

healthy college students were recruited for Experiment 2. The same paradigm as Experiment 1 was used, except that only one set of stimulus array was presented in the center of the screen (Fig. 4A) to reduce the additional demand for attention resource. Meanwhile, given that we did not observe systematic differences in pre-stimulation performance across different stimulation sites in Experiment 1, we only administered 3 runs of the visual WM task after stimulation to reduce the fatigue effect and to save participants' time. A short practice session with 12 trials was included before stimulation on each day to familiarize the participants with the task and the response keys. We used the same behavioral indices for attention scope and attention control, and the effect of tDCS was compared on the post-stimulation performance.

Results

Comparing the visual WM performance in Exp. 1 and Exp. 2

Focusing on the VC condition (which was presumably not affected by the stimulation effect), a two-way mixed effect ANOVA revealed a significant attention component-by-experiment interaction ($F(1, 46) = 24.489, p < 0.001$) (Table 2). Further analysis revealed that the attention scope score (K under the “4 targets” condition) for Experiment 1 was significantly smaller than that for Experiment 2 ($t(46) = -4.278, p < 0.001$). This result is consistent with the hypothesis that Experiment 1 involved more attention control and would show lower visual WM capacity than did Experiment 2. Also as expected, the two experiments did not show a significant difference in attention control scores ($t(46) = 0.476, p = 0.636$), presumably because the additional demand for attention affected the “2 targets + 2 distractors” and the “2 targets” conditions equally. Finally, to investigate whether there was a fatigue effect because subjects in Experiment 1 finished 3 runs of the task before stimulation whereas those in Experiment 2 finished only a practice run of 12 trials before stimulation, we conducted a two-way repeated measures ANOVA with attention component (control vs. scope) and session (before vs. after stimulation) as within-subject measures. Results showed no significant effect of session ($F(1, 26) = 0.001, p = 0.972$) or session-by-component interaction ($F(1, 26) = 0.075, p = 0.787$), suggesting no fatigue effect.

Correlation between the scores of attention control and scope

Consistent with our hypothesis, we found no significant correlation between the scores of attention control and scope after anodal stimulation on the right PPC ($r = -0.076, p = 0.744$) (Fig. 4B) or the right PFC ($r = 0.358, p = 0.111$) (Fig. 4C). A marginally significant correlation was found after VC stimulation ($r = 0.411, p = 0.064$) (Fig. 4D).

tDCS effect on attention control and scope

A two-way repeated measures ANOVA with site (right PFC vs. PPC vs. VC) and attention component (control vs. scope) as within-subject measures showed a significant interaction between attention component and stimulation site ($F(2, 40) = 17.039, p < 0.001$). One-way ANOVA on attention scope using stimulation site as the within-subject factor showed a significant main effect ($F(2, 40) = 12.643, p < 0.001$). Post hoc paired-t tests showed that, compared to VC stimulation, stimulation on the right PPC significantly enhanced attention scope ($t(20) = 4.916, p < 0.001$), but stimulation on the right PFC did not ($t(20) = 1.015, p = 0.322$). The former effect was significantly larger than the latter effect ($t(20) = 3.817, p = 0.002$) (Fig. 5B).

A similar ANOVA on attention control showed a significant main effect of stimulation site ($F(2, 40) = 9.364, p < 0.001$). Post hoc paired-t tests showed that, compared to VC stimulation, stimulation on the right PFC significantly enhanced attention control ($t(20) = 2.779, p = 0.023$),

but stimulation on the right PPC did not ($t(20) = -1.278, p = 0.216$). The two effects were significantly different ($t(20) = 4.313, p = 0.001$) (Fig. 5A). These results revealed a clear double dissociation of right PFC and PPC stimulations: Whereas stimulation of the right PFC improved attention control but not attention scope, stimulation of the right PPC showed the opposite pattern.

As can be seen here, Experiment 2 replicated Experiment 1 in showing that right PPC stimulation enhanced attention scope, and right PFC stimulation enhanced attention control. Also consistent with our hypothesis, right PFC stimulation's effect on attention scope was limited to Experiment 1 because its bilateral presentation of stimuli involved greater attention control than did Experiment 2's central presentation.

Performance-dependent tDCS

To examine the performance-dependent tDCS effect with respect to attention scope, we divided the participants into two groups based on their K values in the “4 targets” condition under VC stimulation (which was viewed as the baseline, similar to pre-stimulation baseline in Experiment 1) ($n = 13$ and $n = 8$ for low- and high-performance groups, respectively). A two-way ANOVA on attention scope showed no significant interaction between stimulation site (PFC vs. VC) and performance group ($F(1, 19) < 1, p = 0.538$), suggesting no performance-dependent effect on attention scope.

To examine the performance-dependent tDCS effect with respect to attention control, we divided the participants into two groups based on their attention control score under the VC stimulation ($n = 11$ and $n = 10$ for low- and high-performance groups, respectively). A similar two-way ANOVA on attention control showed no significant interaction between stimulation site (PFC vs. VC) and group ($F(1, 19) = 1.273, p = 0.273$). These results suggest that there was no systematic difference in the effects of the right PFC stimulation on attention control for both groups.

Discussion

The present tDCS study examined the dissociated roles of the right PPC and PFC in attention scope and attention control during visual WM. We found that anodal stimulation on the right PPC specifically enlarged attention scope when the number of targets reached or exceeded the visual WM capacity. In contrast, tDCS on the right PFC specifically improved attention control, especially when stimuli were presented in the center of the screen. Taken together, these two experiments converged to provide clear causal evidence for the separate roles of right PPC and right PFC in visual WM.

Our results seem to be consistent with a previous TMS study, which found dissociated roles of the PPC and PFC in verbal WM (Postle et al., 2006). In particular, they found that rTMS on the PFC was associated with worse performance in the manipulation but not storage of mental representations in a verbal WM task. In contrast, rTMS on the SPL was associated with worse performance in both active manipulation and passive storage of verbal information. Although active manipulation used in Postle et al. (2006) and the filtering-of-the-distractor manipulation used in our task involve different cognitive processes, they are both associated with attention control. This argument is in line with existing findings that verbal and visual WM share common attention-based neural correlates (Brahmbhatt et al., 2008; Majerus et al., 2016; Majerus et al., 2010; Nystrom et al., 2000; Rama et al., 2001).

Our results provide direct evidence that bilateral presentation introduces additional attention control requirement as speculated based on an existing study (Fukuda et al., 2015). First, after excluding the non-target information from the un-cued side, attention scope increased in Experiment 2 compared to Experiment 1. It should be noted that since the attention control score is computed by the difference between the “2 targets” and the “2 targets + 2 distractors”

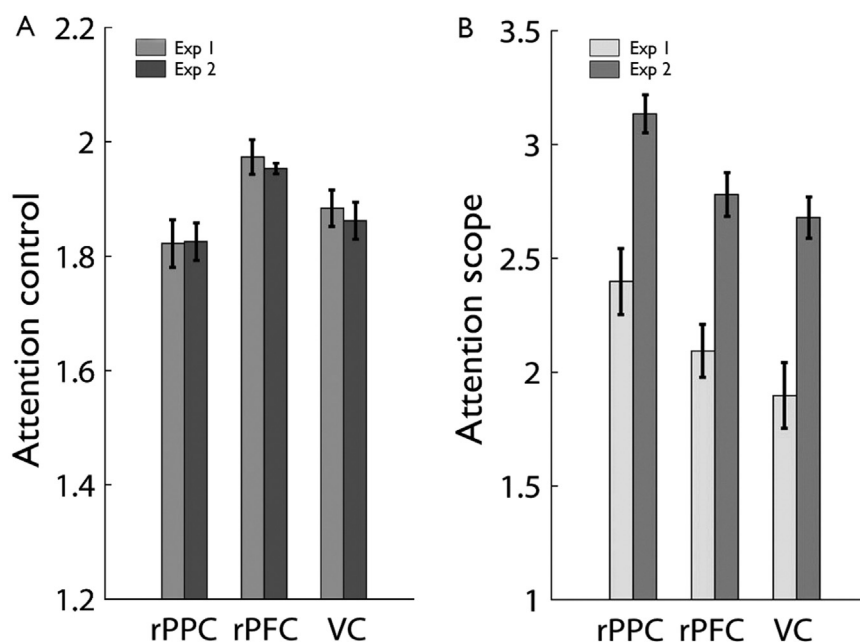


Fig. 5. Post-stimulation performance in two experiments. (A) Attention control indices are plotted as a function of experiment condition and stimulation site for Experiments 1 and 2. (B) Attention scope scores are plotted as a function of experiment condition and stimulation site for Experiments 1 (left) and 2 (right). Error bars denote SEM.

conditions, and both conditions should be influenced to the same extent by the additional attention demand of bilateral presentation, we did not expect a difference in attention control scores between the two experiments (i.e., two presentation modes). Second, we showed that the indices for attention control and scope were significantly correlated in the bilateral presentation paradigm (Experiment 1), but only marginally correlated in the central presentation paradigm (Experiment 2). Finally, PFC stimulation showed a distinct effect on attention scope, depending on whether attention control was required for the no-distractor condition. These results have implications for our understanding of the role of attention control in WM capacity under different conditions (Conway et al., 2001; Vogel et al., 2005).

Mounting evidence has implied that the PPC plays a critical role in visual WM capacity. For example, fMRI studies show that BOLD signal changes in the PPC during encoding or maintenance periods are modulated by the number of items in visual WM (Cowan et al., 2011; Kawasaki et al., 2008; Todd and Marois, 2004, 2005; Xu and Chun, 2006). Consistently, ERP studies reveal that the CDA, which is modulated by the visual WM load, is found mostly in the posterior parietal and lateral occipital areas (McCollough et al., 2007; Vogel and Machizawa, 2004). Furthermore, these studies have suggested that EEG and BOLD activities from the parietal lobule are correlated with WM capacity both within (Drew et al., 2011; Tsubomi et al., 2013; Vogel and Machizawa, 2004) and across subjects (Fukuda and Vogel, 2009; Vogel et al., 2005).

Several tDCS studies have examined the PPC's causal role in visual WM storage using colors, common objects, or dots as stimuli (Berryhill et al., 2010; Heimrath et al., 2012; Hsu et al., 2014; Jones and Berryhill, 2012; Tseng et al., 2012). As no distractor was included in these studies, the PPC's role in attention control was not examined. Meanwhile, because the central presentation paradigm was used in these studies, it is unclear whether these effects reflected an increase in attention scope or attention control, both of which can contribute to WM performance. The present study extends these studies by clearly dissociating the attention control and attention scope processes. We found that right PPC stimulation only improved visual WM performance under the no-distractor condition, providing strong evidence for its specific role in attention scope.

A recent meta-analysis of the effect of PPC tDCS on visual WM

capacity suggests that there was no reliable tDCS effect as a whole (Horvath et al., 2015). Instead, several studies have shown the performance-dependent tDCS effect, with a stronger effect for low-performance healthy participants (Tseng et al., 2012) and for participants who suffer visual WM deficits, such as older adults (Berryhill and Jones, 2012) or AD patients (Boggio et al., 2009). In contrast, the current study found strong tDCS effects for all participants. One important explanatory factor of this discrepancy may be task difficulty (Jones and Berryhill, 2012). In the current study, the orientation of the bars was randomly selected from 0° to 360°, which requires finer-grained mental representations of the stimuli. In addition, subjects needed to continuously switch between the distractor and the no-distractor condition. These design features could have increased the task difficulty. As a result, our healthy, highly educated Chinese college students showed low visual WM capacity compared to subjects in other studies (Tseng et al., 2012). In Tseng et al.'s (2012) study, the K in the sham condition ranged from 1.2 to 5.6 items with a median of 3.7 items. In contrast, the maximum K of VC stimulation in the current study was 3.556 items (K range: 0.311–3.556 items, median=2.244 items). Other studies also showed that motivation and its interaction with strategies might modulate the tDCS effect (Jones et al., 2015). A monetary reward enhanced the anodal tDCS effect for both low and high performers, whereas tDCS only facilitated high performers in the low-motivation condition as compared to the sham condition; and the active strategy facilitated the anodal tDCS effect as compared to the passive strategy for high performers under the low-motivation condition. Future research should further examine the factors that may modulate the tDCS effect.

The exact role of the PPC in visual WM attention scope needs to be further studied. The PPC region has been posited as a common “visual sketchpad” to maintain both object content and spatial information during WM (Baddeley and Hitch, 1974; Xu, 2007, 2009; Xu and Chun, 2006). Consistently, recent studies using multiple voxel pattern analysis to probe the content representation suggest that the posterior parietal cortex could represent trial-specific information held in the memory (Christophel et al., 2012) but not the task-related attention state (Nelissen et al., 2013). In contrast, other studies argue that PPC activity might reflect the overall attentional resource, but not necessarily the maintenance of information itself (D'Esposito and Postle, 2015;

Eriksson et al., 2015). For example, item-specific information is consistently decoded from the activation pattern in the domain-specific visual cortex (Christophel et al., 2012; Nelissen et al., 2013; Riggall and Postle, 2012), but the parietal cortex contains more abstract information such as different task rules (Riggall and Postle, 2012). A recent study suggests that unlike the representations in the primary visual areas, parietal representations were more goal-directed and less affected by distractors during the delay (Bettencourt and Xu, 2016). Therefore, it remains to be determined whether tDCS stimulation enhanced memory capacity by modulating the quality of representation in the parietal lobule and/or its interaction with the posterior visual cortex.

In contrast to PPC stimulation, PFC stimulation facilitated visual WM attention control, which suggests a causal role of this brain region in allocating available cognitive resources to task-relevant information (Chatham et al., 2014). Early lesion and fMRI studies suggested that the PFC could be the neural substrates underlying the central executive process (D'Esposito et al., 1995; Funahashi et al., 1993; Knight et al., 1995; Miller and Orbach, 1972). For example, the PFC is reported to be involved in the maintenance and manipulation of information by selecting representations, but not the locus of stored memory representations (Rowe et al., 2000). Lesions of the PFC reduced patients' behavioral performance in visual WM by disturbing their neural representation for distractors (Voytek and Knight, 2010).

In particular, the PFC may function as a selective mechanism to control the access to goal-directed attention (D'Esposito and Postle, 2015). It could enhance the salience of relevant information or inhibit irrelevant information (Chatham et al., 2014; Gregoriou et al., 2014; McNab and Klingberg, 2008; Rowe et al., 2000). Lesions or virtual lesion of the PFC with TMS resulted in a greater spatial overlap between scene- and face-evoked activities in the extrastriate cortex during a WM task (Lee and D'Esposito, 2012; Miller et al., 2011). Frontal and basal ganglia activity contributed to inter-individual differences in visual WM capacity by exerting control over the access to visual WM attention (McNab and Klingberg, 2008). Cathodal tDCS stimulations on the frontal cortex showed a strong effect on the shifting of attention guided by the cue in a change detection task (Tanoue et al., 2013). Our brain stimulation data revealed that the PFC specifically enhanced visual WM under the distractor condition, which corroborates and extends existing imaging and stimulation findings to suggest that the PFC contributes to attention control in visual WM.

According to Kane and Engle (2002), attention control is the ability to actively maintain relevant information and block or inhibit irrelevant information. In a series of studies, they found that WM capacity was highly correlated with individuals' cognitive control ability, such as response inhibition (Kane et al., 2001). Consistent with this finding, many studies have found that right PFC stimulation improves response inhibition and selective attention (Lee and D'Esposito, 2012; Reinhart and Woodman, 2014; Wu et al., 2014). A recent study of ours found that right PFC stimulation but not right PPC stimulation enhanced both proactive and reactive inhibitory control in a stop signal task (Cai et al., 2015). Taken both studies together, our results provided strong evidence to suggest a specific role of right PFC in attention control.

Although we found that the frontal and parietal cortices played dissociable roles in visual WM, these functions are likely to be highly integrated. The fronto-parietal network (FPN) is proposed to serve as the flexible hub for cognitive control (Zanto and Gazzaley, 2013). For example, FPN synchronization was showed to be critical for visual WM and visuospatial attention (Salazar et al., 2012; Szczepanski et al., 2014). Furthermore, connectivity of these two regions was modulated by WM load (Ma et al., 2012) and individuals' visual WM capacity (Zhang et al., 2016). Computational and imaging evidence further suggests that the excitatory prefrontal input could boost parietal capacity, especially under a high-load condition of visual WM tasks (Edin et al., 2009).

Several questions remain to be answered in future studies. First,

due to the limited spatial resolution of tDCS, we could not pinpoint further functional dissociations within the PFC and PPC. For example, fMRI studies have suggested that the DLPFC (Feredoes et al., 2011; Kundu et al., 2015) and IFG (Feredoes et al., 2006; Zanto et al., 2011) show different top-down regulations on the parietal or occipital cortices during working memory tasks. Within the PPC, the activation of inferior IPS tracked a fixed number of to-be-remembered items regardless of object complexity, while superior IPS tracked the number of items in visual WM storage as feature complexity changed (Xu and Chun, 2006). Similarly, lesions of the posterior and middle IPS segment impaired selection between competing stimuli (Vandenberghe et al., 2012). Combining a meta-analysis of fMRI and functional connectivity data, Nelson et al. (2010) found that left lateral parietal cortex (LLPC) can be divided into different sub-regions that are implicated in different functions such as familiarity judgment, attentional control, re-instantiating context-specific perceptual information, and post-retrieval monitoring. Future studies should use higher-definition tDCS or TMS to further examine this important issue.

Second, future studies should combine tDCS and brain measures such as ERP (Hsu et al., 2014) or fNIRS (Jones et al., 2015) to examine the underlying neural mechanism of tDCS's effect on attention scope and attention control. Third, as WM is temporally separated into encoding, maintenance, and retrieval phases, future studies should also investigate cognitive processes and neural correlates associated with different phases of WM. Finally, besides attention scope and attention control, several other processes, such as prospection, perceptual representations, and long-term memory representations, could all contribute to WM (Eriksson et al., 2015), so more studies are needed to examine the frontal and parietal lobules' roles in these processes.

To conclude, this tDCS study demonstrates dissociable roles of the right PPC and right PFC in visual WM attention scope and attention control. These findings extend our understanding of cognitive and neural mechanisms underlying visual WM. The positive effect of anodal stimulation in the frontoparietal brain regions in enhancing visual WM capacity has potential implications for interventions with individuals who show impaired WM.

Acknowledgments

This work was sponsored by the National Natural Science Foundation of China (31130025), the 973 Program (2014CB846102), the 111 Project (B07008), and the NSFC project (31521063).

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