



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

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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

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