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Dissociable causal roles for left and right parietal cortex in controlling attentional biases from the contents of working memory

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ABSTRACT

The contents of working memory (WM) steer visual attention, but the extent of this guidance can be strategically enhanced or inhibited when WM content is reliably helpful or harmful to a visual task. Current understanding of the neural substrates mediating the cognitive control over WM biases is limited, however, by the correlational nature of functional MRI approaches. A recent fMRI study provided suggestive evidence for a functional lateralization of these control processes in posterior parietal cortex (PPC): activity in left PPC correlated with the presentation of WM cues that ought to be strategically enhanced to optimize performance, while activity in the right PPC correlated with the presentation of cues that ought to be inhibited to prevent detrimental attentional biases in a visual search. Here, we aimed to directly assess whether the left and right PPC are causally involved in the cognitive control of WM biases, and to clarify their precise functional contributions. We therefore applied 1 Hz repetitive transcranial magnetic stimulation (rTMS) to left and right PPC (and a vertex control site) prior to administering a behavioral task assessing WM biasing control functions. We observed that the perturbation of left PPC eliminated the strategic benefit of predictably helpful WM cueing, while the perturbation of right PPC amplified the cost of unpredictable detrimental WM cueing. The left and right PPC thus play distinct causal roles in WM–attention interactions: the left PPC to maximize benefits, and the right PPC to minimize costs, of internally maintained content on visual attention.

Introduction

Representations in working memory can influence what we attend in the environment. This can be beneficial when those representations align with current goals (e.g., rehearsing your shopping list in the store helps you locate the apples) but detrimental when WM contents conflict with goals (e.g., rehearsing your shopping list in the car directs your eyes to a fruit stand, instead of the road). Accordingly, prior studies have found that items in WM can guide attention toward matching—but goal-irrelevant—items in a perceptual task (Soto et al., 2008). When a visual search is performed during a WM delay, for instance, performance profits if a memory-matching item cues a search target (valid WM-benefit), and is impaired if a memory-matching item cues a distractor (invalid WM-cost). When the proportions of valid and invalid trials are manipulated, however, a high proportion of valid trials amplifies the WM-benefit, while a high proportion of invalid trials reduces the WM-cost (Carlisle and Woodman, 2011; Kiyonaga et al., 2012). People, thus, use foreknowledge about WM validity to control the strength of WM biases of attention. This adaptive ability would be critical to optimizing the use of material that is currently on one's mind, so that it can be exploited when it is beneficial to immediate demands in the environment, but kept in check when it is counter-productive.

How does the human brain implement this cognitive control over the linkage between WM and attention? We recently manipulated the predictability (i.e., proportion) of valid and invalid WM cues, during fMRI, to examine WM delay control signals involved in enhancing or inhibiting the influence of WM content in a visual search (Soto et al., 2012). Predictably helpful (i.e., valid) WM cues activated the left posterior parietal cortex (PPC), while predictably distracting (i.e., invalid) cues engaged the right PPC (both relative to a non-predictive baseline, Fig. 1C). These findings suggest a neural dissociation of cognitive control processes associated with enhancement and inhibition of WM biases, giving rise to the intriguing hypothesis of a lateralization in human PPC according to the manner in which WM content is strategically employed to control attention.

The PPC is a heterogenous region that has been implicated in the goal-oriented, flexible control of behavior to meet a variety of cognitive demands (e.g., Duncan, 2010). While there is some support for separable roles of the left and right PPC in such functions as bottom-up attentional orienting either toward or away from salient stimuli (Mevorach et al., 2006), the evidence for hemispheric specialization of attentional

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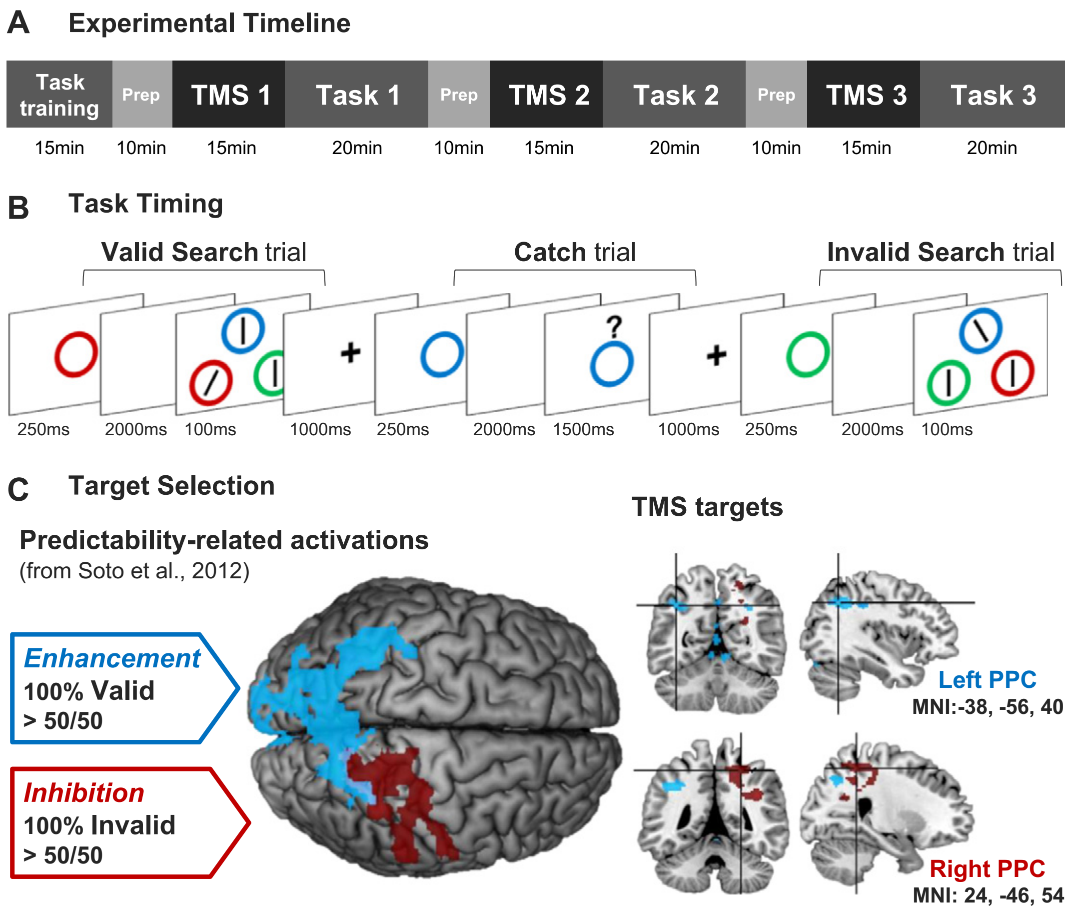

Fig. 1. Experimental methods. A) Before each task run, 1 Hz rTMS was delivered to one of three targets locations—vertex, left PPC, or right PPC—in counterbalanced order. B) After each colored circle memory cue, participants saw either a visual search or a memory probe (i.e., catch trial). Blocks of trials were either 100% valid, 100% invalid, or 50% valid/50% invalid. C) Stimulation sites based on prior fMRI findings.

processes has been mixed. Other studies have suggested, for instance, greater *relative* involvement of the left PPC in oculomotor attention, and the right PPC in attentional orienting (Rushworth et al., 2001a), though not necessarily qualitatively distinct contributions from that of the contralateral hemisphere. Here we perturb normal brain activity, using repetitive transcranial magnetic stimulation (rTMS), to determine the specific and causal roles of the left and right PPC in controlling the relationship between internal WM content and externally-geared visual attention.

We applied 1 Hz rTMS to left and right PPC guided by activation peaks from the prior fMRI study (Soto et al., 2012). This rTMS protocol is generally found to temporarily reduce task-related cortical excitability in the targeted region (Pascual-Leone et al., 1998), and can have the behavioral consequence of hampering performance of tasks that rely on that region (Walsh and Cowey, 2000). Participants completed a combined WM cueing/visual search task—wherein we independently manipulated WM validity and predictability—after each stimulation session. If left and right PPC play causal and qualitatively dissociable roles in the cognitive control over WM biases of attention (i.e. enhancement and inhibition based on WM-validity foreknowledge), then left and right PPC rTMS ought to produce distinct modulation of visual search performance based on WM context.

Methods

Participants

Twenty naïve volunteers (10 females, mean age = 26, age range 21–43) gave written informed consent in accordance with the Duke University Health System Institutional Review Board, and were compensated with $20.00 per hour for their participation. Three participants were excluded—2 because of technical problems during their stimulation sessions, and 1 for chance performance on the behavioral task—leaving 17 participants in the final analysis.

Overview of experiment

Participants were first trained on a composite WM-visual search task that we have previously used to examine cognitive control over WM biases of attention (Kiyonaga et al., 2012; Soto et al., 2012). Stimulation targets were based on group activation coordinates from Soto et al. (2012), which were mapped onto individual anatomical images. All participants underwent a 15-minute session of 1 Hz rTMS for each of three target regions: left PPC, right PPC, and a vertex control site. The vertex was used to reproduce the sensations of real TMS and control for any non-specific effects of the stimulation (cf. Pitcher et al., 2008). Order of stimulation was counterbalanced across participants, and each stimulation period was followed by a run of the behavioral task, which lasted between 15 and 20 min, resulting in approximately 30 min in between each round of stimulation (Fig. 1A).

Stimuli and task procedure

Each trial began with a 1000 ms fixation, followed by a 500 ms blank screen, then a 250 ms colored circle memory cue. After a delay of 2000 ms, a visual search display appeared for 100 ms (Fig. 1B). We used this brief display duration to discourage eye movements. The search display comprised three colored circles at the corners of an