

Right Parietal Cortex Plays a Critical Role in Change Blindness

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There is increasing evidence from functional magnetic resonance imaging (fMRI) that visual awareness is not only associated with activity in ventral visual cortex but also with activity in the parietal cortex. However, due to the correlational nature of neuroimaging, it remains unclear whether this parietal activity plays a causal role in awareness. In the experiment presented here we disrupted activity in right or left parietal cortex by applying repetitive transcranial magnetic stimulation (rTMS) over these areas while subjects attempted to detect changes between two images separated by a brief interval (i.e. 1-shot change detection task). We found that rTMS applied over right parietal cortex but not left parietal cortex resulted in longer latencies to detect changes and a greater rate of change blindness compared with no TMS. These results suggest that the right parietal cortex plays a critical role in conscious change detection.

Keywords: change detection, humans, parietal cortex, rTMS, visual awareness

Introduction

It is well accepted that activity in the occipitotemporal cortex plays a role in visual awareness. Lesions to areas of extrastriate cortex specialized for analysis of a visual attribute give rise to corresponding deficits in awareness for that attribute (for review, see Farah, 1990). These same visual areas have also been associated with reports of awareness in neurologically intact subjects. For example, it has been reported that activity in the lateral occipital complex (LOC) is correlated with subjects' ability to recognize masked objects (Grill-Spector *et al.*, 2000), and left fusiform gyrus and extrastriate areas have also been found to be more active in association with seen versus masked unseen words (Dehaene *et al.*, 2001). Indeed, Milner and Goodale (1995) have argued that ventral stream activation is a necessary condition of awareness. Based on the abilities of a visual agnosia patient, they further suggest that information in the dorsal system can be processed without reaching consciousness.

More recently, however, evidence from fMRI has suggested that the dorsal stream may play a role in visual awareness. In fact, parietal activity has been implicated in visual awareness with a variety of paradigms. For example, Dehaene *et al.* (2001) found that parietal areas were active when subjects were aware of words but not when the same words were masked and thus unseen. Using a binocular rivalry paradigm in which subjects alternately report seeing only one of two incompatible images presented to the two eyes, Lumer *et al.* (1998) not only found that activity in ventral extrastriate areas was correlated with the seen image, in accordance with other research (e.g. Tong *et al.*,

1998), but also that activity in the inferior and superior parietal lobules was enhanced during the perceptual transitions from one image to another. In other words, they found parietal activity when the contents of awareness changed. Similar parietal activation was found during the perceptual transitions that occur when viewing bistable images such as the Necker cube and Rubin's face/vase (Kleinschmidt *et al.*, 1998).

Additionally, using the phenomenon of change blindness, Beck *et al.* (2001) found enhanced activity in the parietal lobe when subjects consciously detected a change but not when they were blind to it. Change blindness can be produced by introducing a brief flicker between successive views of a visual scene (Rensink *et al.*, 1997). Even though the change is large enough to be detected immediately under normal viewing conditions (i.e. without the screen flicker), the flicker paradigm results in long RTs or a complete failure to detect the change. Beck *et al.* (2001) used the flicker paradigm and the resulting change blindness to probe the neural correlates of visual awareness using event-related fMRI. A comparison of trials in which subjects consciously detected a change to trials in which they were blind to it not only revealed enhanced activity in category-selective regions of the ventral visual cortex, as predicted by many neural theories of visual awareness (Logothetis, 1998; Zeki, 2003), but also enhanced activity in bilateral parietal cortex.

However, because fMRI can only reveal an association between activity in a brain region and behavior, it is unclear whether the parietal regions implicated in these experiments play any causal role in awareness. In all these studies, it remains possible that the parietal activity found was a consequence of subjects' awareness and did not play either a necessary or causal role in producing that awareness. One can imagine, for instance, that parietal activity found in the change blindness experiment reflects attention being drawn to the change after the change has been detected and the subject has become aware of it. In order to assess whether parietal activity is in fact critically involved in change detection, we applied rTMS over either right or left parietal cortex (Fig. 1) to transiently disrupt neural activity in these regions (Walsh and Pascual-Leone, 2003), while subjects attempted to detect changes across a brief blank interval (Fig. 2). The peak coordinates of the parietal regions associated with change detection in the fMRI study of Beck *et al.* (2001) were located on each individual anatomical MRI and co-registered with the coil using Brainsight software (Rogue Research, Montreal Canada). If parietal activity plays a causal role in the conscious detection of change, subjects' performance on a change detection task should be selectively worse during rTMS stimulation than during no rTMS stimulation.

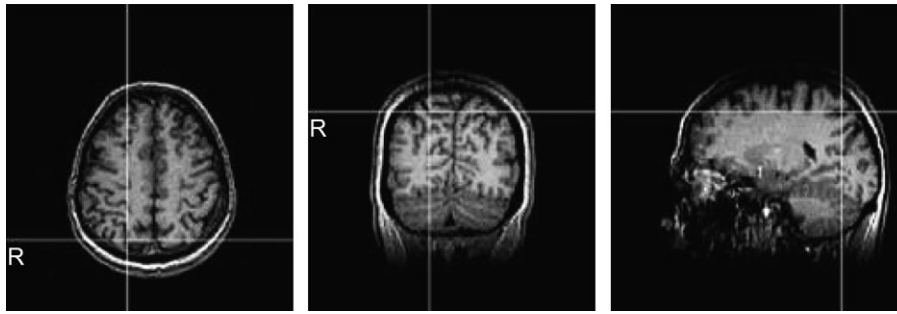


Figure 1. Brainsight localization showing targeted stimulation for the right hemisphere, identified in co-registration with TMS coil position. The region in the crosshairs of the horizontal, coronal, and sagittal views of the brain of a single subject are based on the posterior parietal activation reported in Beck *et al.* (2001) (24, -60, 60 for the right hemisphere and -24, -60, 60 for the left hemisphere).

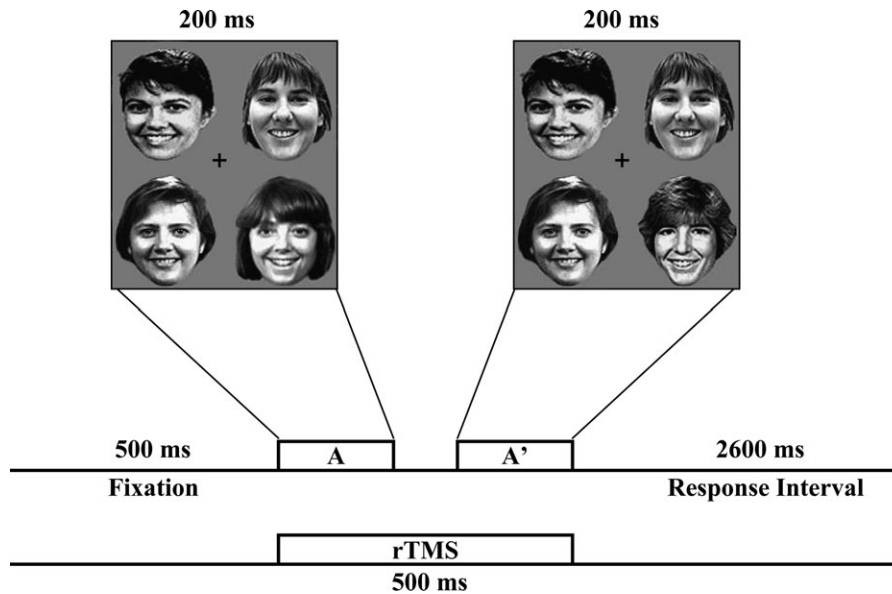


Figure 2. Display and stimulation sequence for a change trial. Each display contained four female faces (chosen from a set of five). A trial consisted of a 500 ms presentation of a fixation cross, followed by two 200 ms displays separated by a 100 ms blank interval. Subjects had 2.8 s to respond whether or not one of the faces changed by pressing one of two buttons on a response pad. In this example, the lower right face changed. All four locations were equally likely, but randomly chosen, to contain the change. rTMS stimulation was time-locked to the onset of the first display and continued for the duration of the visual presentation (500 ms).

Materials and Methods

Subjects

Nine right-handed subjects (three females; age 23–40 years) participated in the study. All subjects were in good health with no past history of psychiatric or neurological diseases and gave their written and informed consent. Subjects had normal or corrected-to-normal vision.

Stimuli and Procedure

Subjects viewed two successive displays of faces in what has been termed the 1-shot task. On each trial the subjects were asked to detect a change between two displays separated by a brief blank interval. A trial consisted of a 500 ms presentation of a fixation cross, followed by two 200 ms displays separated by a 100 ms blank interval. Subjects had 2.8 s from the onset of the second display to respond whether or not one of the faces changed by pressing one of two buttons on a response pad with their right hand. Reaction times were measured from the onset of the second display and responses within 300 ms of the onset of the second display (<1% of all responses) were categorized as premature and excluded from all analyses.

Each display contained four female faces (chosen from a set of five), each subtending $\sim 2.5 \times 2.7^\circ$ of visual angle at a 60 cm viewing distance. The entire display subtended 5.3° horizontally and 5.9° vertically.

On two-thirds of the trials, one of the four faces was replaced by another face in the second display (Fig. 1). All four locations were equally likely, but randomly chosen, to contain the change. The remaining one third of trials did not contain a change.

rTMS Parameters and Design

A Magstim SuperRapid TMS machine, set at 65% of output, and a 70 mm figure of eight coil were used to deliver 500 ms trains of 10 Hz pulses that were time-locked to the onset of the four faces. rTMS was administered in blocks of 60 trials, and subjects received two blocks of each of the following conditions: right parietal TMS, left parietal TMS and no TMS. Block order was randomized with the constraint that each condition occurred once in the first half of the experiment and once in the second half, and subjects began the session with 10 practice trials in which no TMS was delivered. The stimulation site was co-registered with each subject's MRI scan. Brainsight software (Rogue Research, Montreal Canada) was used to identify, in each subject, the Talairach coordinates of the peak parietal activity (i.e. in posterior parietal cortex) previously reported to be associated with conscious change detection (Fig. 2). It should be noted that these are the peak coordinates from the first experiment of Beck *et al.* (2001). Although the peak co-ordinates from the random effects analysis, which included data from the first and second experiment, were slightly different, the extent of the activations

was large enough that the area stimulated by TMS (at the intensities used and with the large figure of eight coil) bears a close correspondence to the activation areas in both experiments.

Results

Mean RTs (to correct trials only) and error rates were computed for each subject as a function of TMS condition (right TMS, left TMS and no TMS) and side of change (right versus left) and entered into a two-way repeated-measures analysis of variance (ANOVA). Figure 3 presents the average of these mean RTs and error rates across participants. The ANOVA on the RTs revealed a significant main effect of TMS condition [$F(2,16) = 43.95$, $P < 0.05$], no effect of side of change or interaction of TMS condition and side of change, $F < 1$. To better understand the main effect of TMS, t -tests comparing right versus no TMS, left versus no TMS, and right versus left TMS were conducted. These analyses revealed that right parietal TMS produced slower change detection responses (819 ms) than no TMS (706 ms) [$t(8) = 2.76$, $P < 0.05$]. Left parietal TMS (714 ms), on the other hand, yielded no impairment relative to no TMS ($t < 1$), and right parietal TMS resulted in significantly slower responses than left parietal TMS [$t(8) = 3.23$, $P < 0.05$]. The direct comparison of

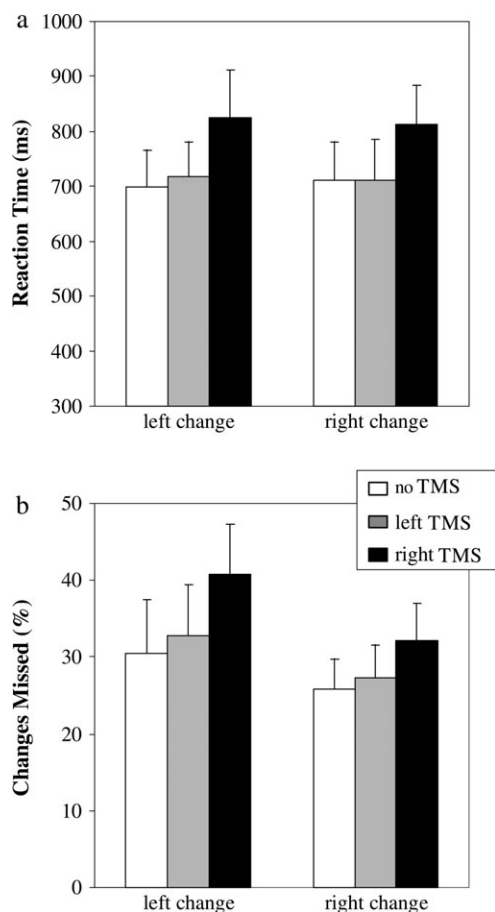


Figure 3. (a, b) Data from right parietal (black bars), left parietal (gray bars) and no TMS (white bars) conditions. Responses within 300 ms of the onset of the second display were categorized as premature and excluded from all analyses. Error bars indicate the standard error of the mean. (a) Mean RTs to changes during right, left and no TMS conditions. RTs were measured from the onset of the second display and do not include incorrect trials. (b) Mean percentage of changes missed during right, left and no TMS conditions. Both measures (a, b) show a clear decrement in performance during right parietal TMS.

the effects of right versus left parietal TMS indicates that the deficit in performance during right parietal stimulation cannot be due to unspecific effects of TMS, because the same stimulation that produced a deficit on the right produced no effect when administered on the left.

Disrupting activity in the right parietal lobe had an adverse effect on the speed with which subjects detected changes, but, more important for the issue of awareness, similar effects were found on accuracy of change detection. The initial ANOVA on the accuracy data, involving all three levels of the TMS factor, revealed a significant main effect of TMS condition [$F(2,16) = 6.16$, $P < 0.05$], no effect of side of change [$F(1,8) = 1.8$, $P > 0.20$] or interaction of TMS condition and side of change, $F < 1$. The subsequent t -tests revealed that right parietal TMS increased the rate of change blindness compared with no TMS [$t(8) = 2.86$, $P < 0.05$]: subjects missed more changes during right parietal stimulation (37%) than during no TMS (28%). As with the RTs, left TMS failed to produce more change blindness (30% misses) than the no TMS condition ($t < 1$), and right TMS resulted in greater change blindness than left TMS [$t(8) = 2.34$, $P < 0.05$]. These analyses included all misses, including those in which subjects failed to respond at all. The same pattern of results, however, was obtained when failures to respond were removed from the analysis. Subjects missed 36% of changes during right TMS, and 30 and 28% of changes during left TMS and no TMS conditions, respectively. In order to assess the effects of TMS on sensitivity of change detection, taking into account false alarm rate as well as hit rate, we transformed the accuracy data into d' . An analysis of the d' data revealed the same pattern of results as the accuracy and RT data. Right parietal stimulation significantly decreased sensitivity to change ($d' = 1.55$) relative to no TMS [$d' = 1.88$; $t(8) = 2.38$, $P < 0.05$] and relative to left TMS [$t(8) = 2.50$, $P < 0.05$], whereas left TMS did not result in a deficit ($d' = 1.88$) compared to no TMS ($t < 1$). Thus, once again the significant effect of right TMS cannot be due to unspecific effects of TMS, because the same stimulation over the left parietal lobe produced no effect.

Eye movement artifacts cannot explain our data either. TMS over posterior parietal cortex (PPC) does not induce eye movements in humans as shown in several TMS experiments on PPC function (e.g. Ashbridge *et al.*, 1997; for review, see Walsh and Pascual-Leone, 2003). Exploratory eye movements on the part of our subjects were also unlikely since the presentation of each array was too brief (200 ms) to complete an eye movement, and anticipatory eye movements between the first and second display to one of the four image positions would have been detrimental to performance: given that the location of the change (if there was one) was random, subjects would have a 75% chance of saccading to the wrong image. Moreover, there is no reason why eye movements of any kind should be present during right posterior parietal stimulation and not left, and yet our performance effects are restricted to the right TMS condition.

Finally, our effects cannot be the result of interference with response selection mechanisms. All subjects made both present and absent responses with their right hand, and given that our effects were also present in the d' measure it would be difficult to explain them in terms of a bias in response. Moreover, although activity in the parietal cortex has been associated with response selection, this activity is lateralized to the left parietal cortex for both left and right-handed responses (Rushworth

et al., 2001a,b; Bunge *et al.*, 2002). Further, the sites associated with response selection are in the supramarginal gyrus whereas stimulation over the sites reported in the present paper had no effect on motor selection (Rushworth *et al.*, 2001a).

Discussion

Hitherto it has been unclear whether the parietal activity found in functional imaging experiments on change blindness was critically involved in the detection of change or whether it was merely a consequence of the detection. The data presented here indicate that the right posterior parietal lobe plays a causal role in the conscious detection of change in a 'change blindness' paradigm. When rTMS was applied over right PPC, subjects not only took longer to detect changes in either visual field they also exhibited a greater rate of change blindness. By *causal* we do not mean that the right PPC gives rise to conscious detection of changes, but rather that it is a critical component. We believe conscious change detection results from an interaction of occipitotemporal cortex and right dorsolateral prefrontal cortex (DLPF) and the PPC (Beck *et al.*, 2001), all of which are necessary components of conscious change detection. It is well established that regions of the occipitotemporal cortex specialized for analysis of a particular visual attribute are necessary for the perception of that attribute, and recently a similar rTMS paradigm to the one used here has shown that right DLPF also plays a causal role in change detection (Turatto *et al.*, 2004).

A causal role for parietal cortex in change detection is in accordance with what is known about change blindness. Change blindness is thought to occur because the transients that would normally be induced by a change in an image are swamped by the larger transient induced by the offset and onset of the displays (Rensink *et al.*, 1997). Thus, in the absence of a clear bottom-up signal, top-down control must be exerted to find the change. There are at least two processes that one might readily associate with detecting a change in a top-down fashion, both of which are compatible with parietal activity. First, a number of researchers have suggested that in order to detect a change in these paradigms the observer must move attention around the image, selecting candidate objects in turn. Indeed, cuing the location of the image that might change dramatically reduces change blindness (Rensink *et al.*, 1997; Scholl, 2000; Driver *et al.*, 2001). In keeping with this, the region in parietal cortex that we stimulated has been consistently implicated in the allocation of attention to stimuli in the visual field (Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002). Second, it also seems necessary that some form of visual short-term memory (VSTM) is involved in change detection. Although the timing used in change blindness paradigms, including the one presented here, is typically shorter than that used for VSTM tasks, the onset of the second display appears to disrupt iconic memory and so a more durable longer lasting form memory is needed. Parietal cortex has been implicated in VSTM tasks, and in particular two groups (Todd and Marois, 2004; Vogel and Machizawa, 2004) found that activity in the PPC is tightly correlated with an individual's storage capacity limit. These data suggest that PPC may be involved in determining what does and does not enter VSTM from a visual scene.

Unilateral Right Parietal Effects

The previous neuroimaging data on this paradigm showed that conscious change detection was associated with bilateral

activation of parietal cortex, but in the current experiment disrupting left PPC had no effect on detection performance. The lack of effect for left parietal TMS, however, is in accordance with neuropsychological studies of the phenomenon of visual neglect in which dramatic deficits in visual awareness predominantly follow right, but not left, parietal lesions (Vallar and Perani, 1986). A number of researchers have suggested that while left parietal cortex directs attention to contralateral space (i.e. the right visual field), the right parietal cortex has a bilateral representation of visual space (Heilman and Van Den Abell, 1980; Mesulam, 1981). This bilateral representation of space would allow the right parietal cortex to take over and compensate for the disruption during rTMS of the left parietal lobe. However, when both hemispheres are intact (as they were in the fMRI experiments) there would be no need for the right parietal lobe to take over the role of the left, and thus bilateral activation would be expected.

Right Parietal TMS Effects on Both Sides of Space

The right hemisphere dominance theory can account for the lateralized effect of TMS, but our data are also in accordance with spatially non-specific functions associated with the right PPC, such as the ability to sustain attention (for review, see Robertson, 2001) and VSTM functions (Duncan *et al.*, 1999; Wojciulik *et al.*, 2001; Pisella *et al.*, 2004; Malhotra *et al.*, 2005). According to the right hemisphere dominance theory, during right parietal disruption, the left hemisphere should still be able to direct attention to the right side of space. However, although performance was slightly better on the right than on the left during right parietal TMS, our data clearly show a pronounced effect of TMS on both the right and left sides of space, implicating these non-spatially lateralized functions of the right PPC. Using a change detection paradigm, Pisella *et al.* (2004) showed that neglect patients with right PPC lesions not only displayed poorer detection performance for changes that occurred on the left than the right (in keeping with a spatial orienting deficit) but they also showed a general deficit in detecting a change in location on either side of space.

A deficit in the ability to sustain attention may also play a role in increasing change blindness, particularly if this interacts with the ability to spatially orient attention (Robertson *et al.*, 1998; Robertson, 2001). If right parietal TMS interferes with subjects' ability to sustain attention over time, they may fail to direct their attention to the location of the change, irrespective of the side of the change. Alternatively, a deficit in sustained attention may interfere with the VSTM component of the change detection task, again irrespective of the side of change.

Because change detection is a complicated process it is unclear which of the functions associated with right PPC are responsible for the effects shown here, indeed it seems likely that they may all play a role. Directing attention to the change may be necessary for encoding the individual images to the level needed to support change detection, or it may be necessary for transfer to VSTM, or for comparing the images in memory. The abilities to maintain the items in VSTM and sustain attention throughout the experiment also seem to be important for change detection. Although future studies, using briefer intervals of TMS at different points in the change detection trial, will help to determine which specific processes are being disrupted by right parietal TMS, it is clear from the current experiment that right PPC plays a critical role in consciously detecting change.

A Role for PPC in Awareness in General

As mentioned in the Introduction, the parietal cortex has been implicated in a variety of tasks that examine visual awareness including binocular rivalry, reversible figures, masking, and change blindness (Kleinschmidt *et al.*, 1998; Lumer *et al.*, 1998; Beck *et al.*, 2001; Dehaene *et al.*, 2001), suggesting that the parietal cortex may play a role in visual awareness in general.

Indeed the processes associated with the PPC are often attributed to awareness more generally, and not just to change detection. If the PPC is responsible for visual short-term storage capacity it is responsible for those items that are ultimately reportable, one of the hallmarks of conscious awareness (Dennett, 1991). Selective attention has also been implicated in visual awareness. It has been known since the 'early selection' experiments of Cherry (1953) and Neisser and Becklen (1975) that selectively attending to a portion of the sensory input renders the observer, for the most part, unaware of the unattended information. More recently, similar conclusions have been drawn from inattention blindness paradigms (Mack and Rock, 1998). But perhaps the strongest evidence for the involvement of the parietal cortex in visual awareness comes from work with neglect and Balints syndrome patients (Robertson *et al.*, 1997; Kim and Robertson, 2001). Both of the syndromes typically involve lesions to the parietal lobes and result in dramatic deficits in awareness.

It is important to note that we are not arguing that the parietal cortex is the neural locus of consciousness, but rather that the functions associated with parietal cortex, such as attention and VSTM, may be necessary prerequisites to visual awareness. Although the data presented here provide evidence that the parietal lobe is critically involved in consciously detecting a change, given the evidence from neglect patients and the fact that the parietal lobe has been repeatedly implicated (although not causally) in other awareness paradigms (Kleinschmidt *et al.*, 1998; Lumer *et al.*, 1998; Dehaene *et al.*, 2001) it seems likely that parietal activity may be necessary for awareness in general. As such, the data presented here are the first to imply that parietal lobe plays a critical role in determining awareness in neurologically intact subjects. Future research into whether this role extends to other paradigms, designed to investigate awareness, will reveal whether parietal activity is in fact a necessary condition for visual awareness in general.

Notes

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