

Opposing roles of sensory and parietal cortices in awareness in a bistable motion illusion



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ABSTRACT

Motion-induced blindness (MIB) is a bistable visual phenomenon in which stationary disks surrounded by a moving pattern intermittently disappear from the viewer's awareness. We explored the cortical network that subserves the MIB phenomenon by targeting its constituent parts with disruptive transcranial magnetic stimulation (TMS), in the form of continuous theta burst stimulation (cTBS). Previous neuroimaging and TMS studies have implicated the right posterior parietal cortex (rPPC) in perceptual transitions such as binocular rivalry, while the visual area V5/MT has been suggested to play a key role in MIB. In this study, we found that cTBS applied to the rPPC lengthened the duration of disappearance in MIB, while cTBS applied to V5/MT shortened the duration of disappearance and decreased the frequency of disappearance in MIB. These results demonstrate a causal role for both the rPPC and V5/MT in MIB, and suggest that the rPPC is involved in shifting resources between competing functional areas, while V5/MT processing initiates and maintains MIB.

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1. Introduction

Motion-induced blindness (MIB) is a striking visual illusion (Bonneh & Donner, 2011). In MIB, high-contrast, stationary disks (presented within a rotating pattern composed of randomly distributed small elements producing coherent directional motion) are perceived as alternately disappearing and reappearing for periods of several seconds (Bonneh, Cooperman, & Sagi, 2001). Traditionally, MIB has been thought to result from a competitive interaction between the static disks and moving background, wherein the latter dominates over the former in a winner-takes-all competition, due to disruption of the fast attentional switching between various objects in a visual scene that is, ordinarily, largely unnoticed (Bonneh et al., 2001).

MIB is one of the few psychophysical phenomena that have been usefully exploited in order to study the neural basis of visual awareness. It is also a compelling example of multistable perception, in which physically invariant stimulation leads to fluctuations in perception. In this respect, MIB shares features with binocular

rivalry, another phenomenon resulting from attentional competition. Binocular rivalry occurs when different images are presented to each eye simultaneously; rather than being combined into a single percept, each monocular image competes for perceptual dominance. Visual phenomena such as multistable perception, where a constant sensory input elicits different conscious percepts, are particularly effective tools for investigating the processes underlying perceptual awareness (Blake & Logothetis, 2002). Previous studies have suggested the existence of common neural substrates shared by a range of bistable stimuli (for example, the temporal pattern of alternations reported during binocular rivalry is highly correlated with that of MIB; Carter & Pettigrew, 2003). Therefore, in the present study, we focused on MIB as a representative bistable stimulus. The neural basis of binocular rivalry has been localized to visual areas V1, V2, V4, and V5/MT by single unit recordings from the primate cortex (Leopold & Logothetis, 1996; Logothetis & Schall, 1989). Further evidence indicated V1 and V5/MT as the key regions involved in the 'winner-takes-all' contest for perception between the static disks and moving background of the MIB display. For example, when subjects view a MIB display, the perceived reappearance of a disk is associated with an increase in the blood oxygen-level dependent (BOLD) signal in V1 and V2 and a corresponding reduction in activity of the contralateral motion-sensitive areas of the human middle temporal complex (hMT+) (Hsieh & Tse, 2009). Pearson, Tadin, and Blake (2007) demonstrated that on-line transcranial magnetic stimulation (TMS)

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applied to the occipital cortex disrupts conventional binocular rivalry, but has no effect on flicker-and-swap rivalry. This finding suggests that binocular rivalry is mediated by earlier level sensory processing and with different neural correlates compared to other types of perceptual rivalry.

A number of studies have used TMS to investigate the causal role of the parietal areas in bistable perception (Carmel, Walsh, Lavie, & Rees, 2010; Funk & Pettigrew, 2003; Kanai, Bahrami, & Rees, 2010; Kanai, Carmel, Bahrami, & Rees, 2011; Zaretskaya, Thielscher, Logothetis, & Bartels 2010).

Funk and Pettigrew (2003) found that single pulse TMS applied to either the left or right PPC reduced the time to switch from appearance to disappearance, or vice versa; this result was consistent with Bonneh's original view that the parietal attention areas are involved in MIB. Moreover, the disruption of activity via TMS in different subregions of the parietal cortex appears to result in different, often opposing effects (increasing or decreasing of reversal rates), suggesting that the parietal network subserving bistable perception, although complex, operates at a resolution that can be probed successfully with TMS (Kanai et al., 2011).

In summary, 2 main causal elements in perceptual rivalry have been proposed: an early visual process (Blake, 1989; Tong & Engel, 2001) and higher-level or 'top-down' operations (Kovacs, Papathomas, Yang, & Feher, 1996; Logothetis, Leopold, & Sheinberg, 1996); this suggests that perceptual rivalry is a complex, multilevel process (Blake & Logothetis, 2002). In this context of multilevel processes, we used the MIB phenomenon to investigate the causal role of V5/MT and rPPC in visual processing in healthy subjects, by disrupting activity in these brain areas using high-frequency repetitive TMS (continuous theta burst stimulation, cTBS) delivered immediately before subjects performed a perceptual task. This particular TMS protocol allows the disrupting effects to outlive the period of stimulation and to last for the entire duration of the experimental session (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005; Vallesi, Shallice, & Walsh, 2007). Given the disruptive effect of cTBS to cortical processing, we expected the MIB effect to weaken following cTBS to V5/MT. We also predicted dissociation between this and the effect of cTBS applied over the rPPC, an area that dampens MIB duration by allowing attention to switch back and forth between display elements (Bonneh et al., 2001; Schölvinck & Rees, 2009).

2. Materials and methods

2.1. Participants

Fifteen healthy volunteers (12 men and 3 women) aged between 22 and 52 years, with normal or corrected-to-normal vision, and with no history of neuropsychiatric disorder participated in the experiments. Subjects were unaware of the purpose and hypotheses of the experiments. All participants gave their written informed consent prior to their inclusion in the study. This study was conducted in accordance with the Declaration of Helsinki, and was approved by the local ethics committee. All participants had previous experience with TMS through participation in previous studies. Ten participants took part in the first stimulation site condition (V5/MT), 8 in the second stimulation site condition (rPPC), and 8 in the control condition (NO cTBS). Two participants took part in all 3 stimulation site conditions, 2 in the first and the second stimulation site conditions, and 5 in the first and the third stimulation site conditions. One participant withdrew after one of the experiments due to discomfort caused by the MIB visual stimuli. Aiming at using a conservative approach, we considered the three stimulation site conditions as a between-subjects factor.

2.2. Stimuli and procedure

The MIB stimulus is shown in Fig. 1. Stimuli were presented on a 24-in. CRT display (GDM-FW900 flat widescreen, Sony, Japan) with a resolution of 2048 H × 1536 V pixels, where 1 pixel subtended 0.0062 degrees of visual angle. The vertical refresh rate was set at 75 Hz. The approximate viewing distance was 1.5 m, and all stimuli were presented on a black background. A $2.94 \times 2.94^\circ$ area of 49 equally spaced blue cross elements (The Commission Internationale d'Eclairage

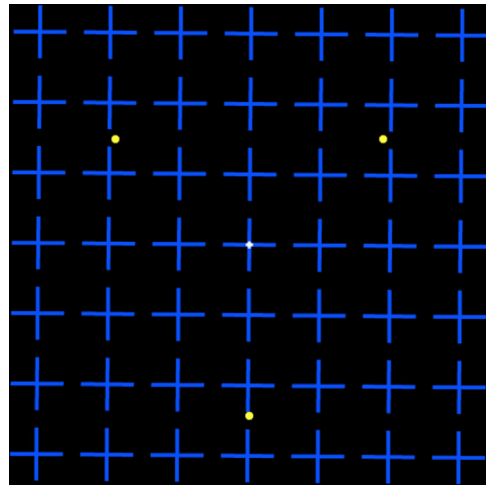


Fig. 1. The MIB stimulus display. As shown, 3 static yellow disks were presented on a grid formed of blue crosses that rotated counter-clockwise at $120^\circ/\text{s}$. The grid measured $2.94 \times 2.94^\circ$ and consisted of 49 equally spaced blue cross elements at a viewing distance of 150 cm.

(CIE) chromaticity coordinates $x=0.161$, $y=0.0989$, luminance 5.14 cdm^{-2}) was rotated around a centre-point at a rate of $120^\circ/\text{s}$ on a black background (0.37 cdm^{-2}). Superimposed on the grid were 3 static yellow disks (CIE chromaticity coordinates $x=0.412$, $y=0.493$, luminance 83.3 cdm^{-2}), equally spaced on an imaginary circle with a radius of 1.09° . The size of each yellow disk was 0.0764° . A personal computer running Windows XP was used to control the presentation of stimuli and the collection of data. Stimuli were generated by Presentation 11.0 software (Neurobehavioral systems Inc., Albany, CA, USA).

Participants were seated on a comfortable chair in a dark room and asked to steadily fixate on a centrally displayed white cross (100 cdm^{-2}) for blocks of 5 min. Participants were instructed to press and hold down the corresponding key ('1' for left upper disk, '2' for right upper disk, and 'space' for bottom disk) on the keyboard in response to the disappearance of yellow disks (which appeared at the same pre-chosen locations around the fixation cross), and to release the button when any one of the disks had reappeared. Thus, at any given moment, any, all, or none of the keys could be pressed or released. The duration between key press and corresponding key release was recorded as the perceived disappearance time. Practice trials were performed prior to behavioural recording to ensure that the participants adequately understood the task.

2.3. TMS stimulation and site localization

TMS was administered using a Magstim Super Rapid Stimulator (Magstim, UK). The coil was a figure-of-eight coil (70 mm outer wing diameter). Participants performed a baseline block and a post-cTBS block (but note that, in fact, the control group did not receive cTBS). The interval between the 2 blocks was 1 h. The order of presentation of baseline and post-cTBS blocks was counterbalanced between subjects.

In the first stimulation site condition, V5/MT was targeted with cTBS. V5/MT was localized using a functional method in which the centre of the coil is placed on the surface of the skull such that the stimulation elicits phosphenes that intrude on the centre of the visual field, i.e. the disk location (for a discussion of this method see Walsh & Pascual-Leone, 2003). The starting location for stimulation was 2 cm dorsal and 4 cm lateral from theinion. The coil was then moved slightly in order to determine the optimal position from which phosphenes could be induced (the reliability of this method for locating V5/MT has been previously demonstrated by Stewart, Battelli, Walsh, and Cowey (1999)). Due to the size of the cortical surface area covered by the figure-of-eight coil, it is likely that the satellites of V5/MT (e.g. MST) are also affected by this stimulation.

Following determination of the stimulation site, cTBS was delivered at this site, using an intensity of 75% of the phosphene threshold, with the coil handle pointing downwards and parallel to the midsagittal plane. TBS consisted of trains of 3 TMS pulses that were triggered by square waves of 1-ms duration, repeated every 20 ms (50 Hz frequency); each train was repeated every 200 ms (5 Hz). cTBS consisted of uninterrupted repetition of trains for 40 s (600 pulses). Detailed descriptions of these TMS paradigms have been provided elsewhere (Huang et al., 2005).

In the second stimulation site condition, the rPPC was targeted with cTBS. Baseline and cTBS blocks were identical to those in the first stimulation site condition. The site of cTBS for rPPC was determined by frameless stereotaxy using a Polaris infrared tracking device (Northern Digital, Waterloo, Ontario, Canada) andBrainsight software (Rogue Research Inc., Montreal, Quebec, Canada). Whole-head

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