

Note

Unconscious vision in action

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Abstract

The dorsal visual processing stream has been suggested to be involved with the unconscious processing of visual information for visually guided actions. In this study, transcranial magnetic stimulation (TMS) was used to gate input into the dorsal visual processing stream by disrupting primary visual cortex (V1) function. Despite restricting geniculostriate processing contributions in the dorsal stream, consistent effects on reaching performance from unconscious visual events were nonetheless measured. These results suggest a functionally intact, albeit unconscious, projection to the dorsal pathway that bypasses V1 and implicates a functional input into the dorsal stream from the superior colliculus.

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1. Introduction

In our everyday lives, we infrequently reach out and grasp an object that we have no intention of using. For example, when preparing a meal, we may suddenly be surprised to find a tin can opener in our hands when trying to open a glass jar. Such instances suggest that our visual and motor systems may be independently linked from conscious perception. The mechanisms underlying these visual ‘zombie’ processes have been under intense investigation and have provided some insights into the neural basis for unconscious vision (Milner & Goodale, 1995). In particular, the dorsal visual processing stream has been suggested to be involved with the coding of visual object locations (Ungerleider & Mishkin, 1982), and more recently, for visually guided actions (Goodale & Milner, 1992).

The primary evidence for dorsal stream involvement in vision for action comes from demonstrations of preserved reaching and motor control abilities in a patient with apperceptive visual object agnosia after bilateral ventral, but not dorsal visual cortex damage (Goodale, Milner, Jacobson, & Carey, 1991; James, Culham, Humphrey, Milner, & Goodale, 2003). In addition to dorsal stream projections from the visual cortex, several anatomical studies have also demonstrated a small proportion of direct

retinal projections into the superior colliculus, which in turn sends projections through the pulvinar nucleus of the thalamus to the posterior parietal cortex of the dorsal stream (Kaas & Huerta, 1988; Robinson & McClurkin, 1989). Thus, influences on visually guided actions may be a consequence of dorsal stream projections from both the retinogeniculostriate and retinotectal pathways. In this study, I tested the hypothesis that information processing within the retinotectal pathways alone is sufficient to influence visually guided actions in humans.

To assess this hypothesis, a remote distractor paradigm was adapted to be used in a visually guided reaching task. In this paradigm, a visual distractor typically produces saccadic eye movement onset delays to a simultaneously presented target (Rafal, Smith, Krantz, Cohen, & Brennan, 1990; Ro, Shelton, Lee, & Chang, 2004; Walker, Deubel, Schneider, & Findlay, 1997). However, when simple button press reaction times to the onset of two simultaneously presented targets are measured, responses are faster when an additional target is presented, a phenomenon referred to as the redundant target effect (Marzi, Tassinari, Aglioti, & Lutzemberger, 1986; Miller, 1982). Interestingly, both the onset delays in saccades from remote distractors and the decreases in response times for button presses from redundant targets have been measured without awareness of the additional stimulus (see Rafal et al., 1990; Ro et al., 2004 for saccades; and Marzi et al., 1996; Savazzi & Marzi, 2002; Tomaiuolo, Ptito, Marzi, Paus, & Ptito, 1997 for button presses). In addition to assessing any effects of unconscious stimuli on

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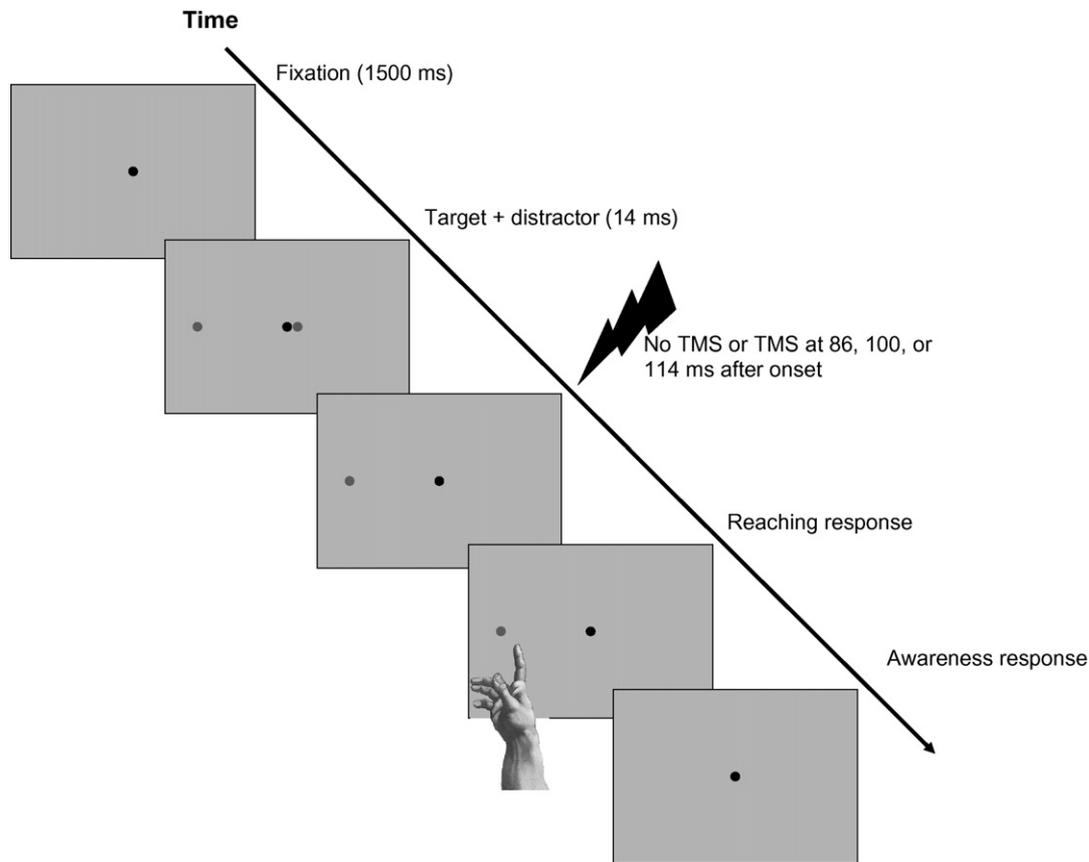


Fig. 1. The stimuli, timing, and procedures for the main experiment.

reaching performance, this study also examined whether delays in reaching onset, as with saccades, or whether faster reaching onset latencies, as with manual button presses, are induced from an additional visual stimulus presented along with a target.

2. Methods

Transcranial magnetic stimulation (TMS) over the primary visual cortex was used to induce a transient visual suppression and to limit visual information processing to non-geniculostriate visual pathways. Prior to commencing the main experiment and after informed consent, a visual cortex localization task was performed in each of the six participants (mean age = 25.8; 2 males). TMS was conducted using a Cadwell Laboratories (Kennewick, WA) MES-10 stimulator (2.2T maximum output) connected to a 9 cm circular coil. The coil was initially positioned approximately 2 cm above the inion and TMS was administered 100 ms after a green dot was briefly (16.7 ms) presented at the center of a 17 in. Sony Trinitron monitor. If the dot was perceived on at least 3 of 5 trials, the coil position, timing, and intensity was adjusted until at least 3 of 5 stimuli went undetected. The lowest intensity at which 3 of 5 visual stimuli were suppressed was defined as the threshold intensity (mean = 56%). TMS was set at 10% above the threshold intensity for the main experiment and was administered on 75% of the trials with equal probability at 86, 100, or 114 ms after the visual target onset. These parameters typically induce a small (approximately 1°) and transient (approximately 50 ms) scotoma in the central visual field, which can be measured by time-locking briefly presented visual stimuli near or at fixation (Amassian et al., 1989; Corthout, Uttl, Walsh, Hallett, & Cowey, 1999; Ro, Breitmeyer, Burton, Singhal, & Lane, 2003).

In the main experiment, the target stimulus was a green dot (0.2° of visual angle) that appeared 5° or 10° to the left or right of fixation (see Fig. 1). The irrel-

evant visual stimulus, which was displayed on half of the trials, was identical to the target stimulus and positioned 0.1° to the right of fixation, at the location of the TMS-induced scotoma. The target stimulus remained on the screen until the end of the trial, whereas the irrelevant visual stimulus appeared simultaneously with the target, but remained present for only 14.2 ms. On each trial, the participants were asked to provide two responses. First, they were asked to respond by reaching to the target stimulus as quickly and as accurately as possible, while ignoring the irrelevant visual stimulus and the TMS pulse when they were presented. After their motor response, the participants were then asked to report whether or not they perceived the additional central stimulus that was presented on half of the trials. This latter response was used to sort trials into aware and unaware responses. Trials on which the irrelevant visual stimulus was presented, but that participants reported its absence due to the TMS induced scotoma were classified as unaware trials. Trials in which a TMS pulse was administered, but the participants accurately detected the central stimulus were classified as aware trials. These aware trials when the TMS pulse was administered were likely due to small variations in visual cortex excitability and/or TMS coil placement, but served as ideal within-subject control trials. Note that all parameters for these aware TMS trials are identical to the unaware TMS trials except for the percept reported by the subject. Following the participants' awareness response on each trial, the next trial commenced after an intertrial interval of 1500 ms. Each participant completed a total of 320 trials.

A Polhemus FASTRAK magnetic digitizer was used to measure the reaching responses. The three-dimensional coordinates of a receiver probe, which was attached to the index finger of the right hand, were digitized, sampled at 120 Hz, and stored for offline analysis. The digitized motion tracking data were subjected to a velocity computation algorithm written in Matlab (Mathworks, Natick, MA). Movement RTs were defined as the earliest time point at which the reaching movement of the hand exceeded 2.5 cm/s in any of the three spatial dimensions. All RTs greater than or less than 2 standard deviations from the mean for each subject were excluded from the analyses. This study was approved by the Institutional Review Board at Rice University.

3. Results

On the no TMS control trials, not surprisingly, participants were highly accurate (94.2%) at detecting the irrelevant visual stimulus and very rarely (0.8%) made a false alarm. In contrast, when TMS was applied over the primary visual cortex, participants made significantly more false alarms (2.1%) on the irrelevant stimulus-absent trials as compared to the no TMS trials (two-tailed $t_5 = 3.50$, $p = .017$). These higher rates of false alarms may be due to the perception of induced phosphenes from TMS of the visual cortex (Covey & Walsh, 2000; Kammer, 1999). More importantly, however, the participants missed over one-quarter of the irrelevant visual stimuli when they were presented within the TMS-induced scotoma (26.7%). The percent detection difference between the TMS and no TMS trials was highly significant (two-tailed $t_5 = 4.54$, $p = .006$).

Signal detection analyses were also conducted on the detection (i.e. hit) and false alarm rates for the irrelevant visual stimulus. There was a significant difference in sensitivity for detecting the irrelevant visual stimulus between the no TMS ($d' = 4.55$) and TMS ($d' = 2.7$) conditions (two-tailed $t_5 = 5.27$, $p = .003$), but no differences in response biases/criterion shifts (both $C_s = .7$; two-tailed $t_5 = 0.37$, $p = .728$). This above chance hit rate ($d' = 2.7$) for the TMS trials reflects the irrelevant visual stimulus being perceived on a large proportion of the trials (73.3%). This was due, in part, to the use of a detection rather than a discrimination task, along with the specific TMS parameters employed in this study. However, since responses were binned according to the reported percept, these aware trials with TMS allowed for a direct comparison of aware versus unaware trials under identical stimulus conditions; the visual and TMS stimuli, timing, and procedures were the same on these TMS trials, but differed only in the reported percept.

To assess the effects of consciousness of the irrelevant visual stimulus on reaching performance, reaction times (RTs) from five different conditions were compared (see Fig. 2). In the no

TMS control trials, the irrelevant visual stimulus significantly facilitated reaching reaction times (RT) to the peripheral target stimulus compared to the irrelevant visual stimulus-absent condition (two-tailed $t_5 = 2.59$, $p = .049$), an effect opposite to that observed with saccadic eye movement responses (Rafal et al., 1990; Ro et al., 2004; Walker et al., 1997). This significant facilitation for the irrelevant visual stimulus-present trials in the no TMS condition was measured despite overall reaction times being numerically, but not statistically longer than the TMS trials, which can be attributed to the warning nature of the TMS pulse (Sawaki, Okita, Fujiwara, & Mizuno, 1999).

Most importantly, when the irrelevant visual stimulus was unconsciously presented within the TMS-induced scotoma (i.e. on all trials when the participant reported not perceiving the centrally presented stimulus), it nonetheless significantly facilitated reaching responses to the peripheral target as compared to the stimulus-absent trials (two-tailed $t_5 = 2.86$, $p = .035$) (see Fig. 2). This significant RT facilitation was measured despite the fact that these stimulus-present, but unconscious trials were phenomenologically identical to the observer as the stimulus-absent trials. Furthermore, RT performance on these unconscious stimulus-present trials was statistically identical to the conscious stimulus-present trials with TMS, where the TMS pulse was not sufficient enough to eliminate the stimulus from visual awareness (two-tailed $t_5 = 0.38$, $p = .723$). No other differences or interactions were significant in the RT data.

The data from the unaware, stimulus-present trials without TMS were not included in this main analysis because two subjects never missed the irrelevant visual stimulus on the no TMS trials and a separate analysis revealed the data from this set of conditions to be too noisy and variable to produce any significant results and meaningful comparisons. Analyses on the movement times, movement amplitudes, and velocity data revealed no significant differences between the different conditions.

4. Discussion

In this study, single-pulse TMS was applied over the visual cortex to disrupt the processing of a centrally presented visual stimulus. When the TMS rendered the participants blind to this centrally presented visual stimulus, influences from this unconscious event were still measured on the reaching reaction times. Thus, these results demonstrate a consistent and reliable effect of unconscious visual stimuli on visually guided actions, as has also been shown in visual masking studies (Binsted, Brownell, Vorontsova, Heath, & Saucier, 2007; Schmidt, 2002). The effects of unconscious vision on reaching were identical to those for conscious vision, suggesting that the primary visual cortex is not necessary for visually guided actions and that restricted input into the dorsal processing stream from other visual processing pathways, such as the retinotectal pathway, may be sufficient for influencing behavior.

While the retinotectal pathway seems the most likely and parsimonious candidate for these unconscious effects on reaching, there may be other pathways or processes that contribute to these results. For example, as in the blindsight literature, in which some studies have suggested islands of spared primary

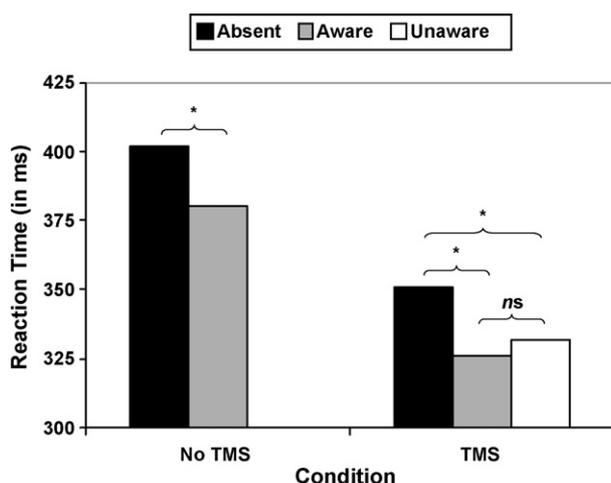


Fig. 2. Effects on reaching from unconscious vision. Regardless of whether participants were aware or unaware of the irrelevant visual stimulus, the presence of the visual stimulus significantly facilitated reaching initiation times. Asterisks indicate $p < .05$.

visual cortex as the neural substrate for the above-chance discrimination capabilities in some patients (Fendrich, Wessinger, & Gazzaniga, 1992; but see Kentridge, Heywood, & Weiskrantz, 1997), it is conceivable that TMS over the visual cortex is sufficient to eliminate a visual stimulus from awareness, but that some aspects of the stimulus may still be processed in V1. Although this study cannot definitively rule out this alternative explanation, it is unlikely for several reasons. First, many studies have now demonstrated that the disruptive effects of TMS over the visual cortex are similar to those measured in patients with scotomas or hemianopias from brain damage (Amassian et al., 1989; Kamitani & Shimojo, 1999; Kammer, 1999; Kastner, Demmer, & Ziemann, 1998). Furthermore, other studies have suggested that the primary visual cortex, and in particular later temporal processing epochs within it, plays an essential role in visual awareness (Lamme & Roelfsema, 2000; Ro et al., 2003). Since the TMS pulse in this study was only administered during the initial feedforward sweeps of visual processing, any residual processing during the effects of the TMS should have entered into awareness after V1 recovery. In fact, the relatively high proportion of hit rates during the TMS trials may have been due to some residual processing in V1 during the effects of the TMS. Thus, the conservative measure of only including the minority of trials on which the participant definitively reported no awareness of the stimulus, rather than inferring unawareness from a separate block of trials in which detection was assessed, further suggests that incomplete primary visual cortex suppression is an unlikely explanation. However, future studies using fMRI in conjunction with TMS of the visual cortex might be informative regarding the extent of processing disruption.

Interestingly, facilitatory rather than interference effects were measured in the reaching initiation times. In a previous study using this distractor paradigm, significant delays were measured for saccadic eye movement and button-press responses (Ro et al., 2004). These opposite results for visually guided reaching under identical visual stimulus conditions demonstrate that the effects of a visual stimulus on behavior are highly dependent upon the response requirements and neural architecture necessary for performing the task. In particular, these results further suggest that differential pathways are likely to be involved with these different visually guided actions, with reaching responses relying upon cortical architecture more than saccadic responses, which under these circumstances may be entirely driven by subcortical processes in the superior colliculus. Further experiments examining the differential effects of visual stimuli on hand and eye movements may provide additional insights into the neural mechanisms of visually guided actions.

In conclusion, the current results shed some further insight into the mechanisms that may be occurring in patients with the phenomenon of blindsight, the above-chance performance on discrimination and reaching responses to stimuli in the blind field after primary visual cortex damage (Weiskrantz, 1996). Although blindsight is seldomly and inconsistently observed (Blythe, Kennard, & Ruddock, 1987; Marzi et al., 1986), these results provide further evidence that the localization of visual objects with reaching or pointing movements may be a con-

sequence of retinotectal projections into the dorsal processing stream that are important for visually guided actions.

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