

Effects of Right Parietal Transcranial Magnetic Stimulation on Object Identification and Orientation Judgments

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Abstract

■ We investigated the role played by the right parietal lobe in object identification and the ability to interpret object orientation, using transcranial magnetic stimulation (TMS) to momentarily interfere with ongoing cortical activity. Short trains of TMS pulses (12 Hz) were applied to a site overlying the right intraparietal sulcus/inferior parietal lobe while subjects performed either object identification tasks (i.e., picture–word verification and categorizing objects as natural or manufactured) or object orientation judgment tasks (i.e., picture–arrow verification and deciding whether an object was rotated clockwise or counterclockwise). Across different tasks, right parietal

TMS impaired orientation judgments, but facilitated object identification, compared to TMS applied to a brain vertex control site. These complementary findings demonstrate that the right parietal lobe—a region belonging to the dorsal visual stream—is critical for processing the spatial attributes of objects, but not their identity. The observed improvement in object recognition, however, suggests an indirect role for the right parietal lobe in object recognition. We propose that this involves the creation of a spatial reference frame for the object, which allows interaction with the object and the individuation of specific viewing instances. ■

INTRODUCTION

One of the fundamental tenets of visual neuroscience is that different visual attributes, such as shape, color, motion, and orientation, are processed in functionally independent modules that are relatively widely distributed across the cerebral cortex. One example of such a functional dissociation is illustrated by the syndrome of *object orientation agnosia* (Harris, Harris, & Caine, 2001; Karnath, Ferber, & Bühlhoff, 2000; Turnbull, Beschin, & Della Sala, 1997). Patients suffering from this syndrome are profoundly impaired at judging the orientation of objects, while at the same time showing intact recognition of objects presented in different orientations. Their difficulties are apparent on tasks that require them to explicitly judge whether an object is in its usual or canonical orientation, as well as on orientation–discrimination tests and when copying or drawing objects from memory. Interestingly, in addition to their high recognition accuracy, these patients' reaction times (RTs) on naming tasks are also insensitive to orientation (Turnbull, Della Sala, & Beschin, 2002), unlike normal observers who typically show a systematic increase in naming times as

objects are rotated further from the upright (Jolicoeur, 1985).

This functional dissociation between the ability to process object identity versus object orientation maps well onto the proposed division of the visual system into a ventral, occipito-temporal, processing stream dedicated to object recognition and a dorsal, occipito-parietal, stream dedicated to spatial perception and the visual control of action (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). Specifically, shape processing leading to object recognition takes place in regions of the ventral visual pathway, notably the inferior temporal lobe in monkeys (Logothetis & Sheinberg, 1996) and the lateral and ventral occipital lobe in humans (Grill-Spector & Malach, 2004). Both of these areas are typically well preserved in patients with orientation agnosia, in keeping with their good recognition skills. At the same time, though, all orientation agnostic patients reported in the literature have evidence of damage to the parietal lobes, more commonly in the right hemisphere (Fujinaga, Muramatsu, Ogano, & Kato, 2005; Harris et al., 2001; Karnath et al., 2000; Turnbull et al., 1997). This suggests that the parietal cortex is critically important for representing the spatial orientation of objects. Neurophysiological and neuroimaging studies also implicate posterior parietal areas, in particular, the inferior parietal lobe and the caudal part of the intraparietal sulcus (cIPS), in orientation coding (Shikata et al., 2001; Sakata, Taira, Kusunoki, Murata, &

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Tsutsui, 1999; Taira, Kawashima, Inoue, & Fukuda, 1998; Faillenot, Sakata, Costes, Decety, & Jeannerod, 1997; Shikata, Tanaka, Nakamura, Taira, & Sakata, 1996; Eacott & Gaffan, 1991). Furthermore, some neuroimaging studies suggest that the right IPS might play a more significant role in this process in humans (Taira et al., 1998; Faillenot et al., 1997), which is consistent with the predominantly right hemisphere pathology of a number of patients with orientation agnosia.

This apparently neat division of labor between a ventral pathway dedicated to shape and object recognition and a dorsal pathway dedicated to spatial analysis and visuomotor integration is challenged by findings of parietal lobe involvement in object recognition. A recent functional magnetic resonance imaging study found almost identical patterns of brain activation in the IPS, as well as in object-related regions of the ventral stream, during tasks that required either object identification or orientation judgments (Altmann, Grodd, Kourtzi, Bülthoff, & Karnath, 2005). However, imaging findings are correlational in nature and do not constitute evidence of a causal role of a brain area in a particular cognitive function. It may be that in these tasks, which required sequential matching of two objects, subjects automatically processed both the identity and the orientation of the objects, even though one of the dimensions was irrelevant to the task at hand. Somewhat more compelling evidence of parietal involvement in object recognition comes from a different category of neurological patients, namely, patients with *apperceptive agnosia* (Warrington & James, 1988; Warrington & Taylor, 1973). After suffering right hemisphere damage, which often encroaches on the parietal lobe, these patients have difficulty recognizing objects presented in rotated or unusual views even though they can recognize objects from canonical views. Thus, apperceptive agnosia does seem to provide some evidence for a causal link between right parietal lobe function and object recognition. However, it is not clear whether apperceptive agnosia should be seen as a true disorder of object recognition. An alternative explanation is that it reflects spatial processing impairments, for instance, a failure to interpret the stimulus as depicting a particular view of an object, that indirectly impinge on the recognition process (Warrington & James, 1988).

A number of recent behavioral studies from our laboratory provide evidence that may speak to this issue. In a series of experiments involving rapid serial visual presentation of objects, we have shown that object recognition proceeds in two stages: a preliminary recognition stage in which the identity of the object is activated in memory via orientation-invariant representations, and a subsequent consolidation stage, which involves binding the object's identity with its orientation at a particular moment in time (Dux & Harris, 2007; Harris & Dux, 2005a, 2005b). The first stage is sufficient to support a variety of implicit recognition phenomena, such as priming and repetition blindness, whereas the second stage

seems to be required for encoding the items for report and individuating different instances of the object. Our experiments suggest that the well-known viewpoint costs associated with recognizing rotated objects (Jolicoeur, 1985) arise during this consolidation stage and are due to an interference between orientation cues extracted from the image and the expected (e.g., canonical) orientation retrieved from memory along with the object's identity (Dux & Harris, 2007; Harris & Dux, 2005b). These findings could provide a rationale for the involvement of spatial routines implemented by the parietal lobe in the consolidation stage of recognition.

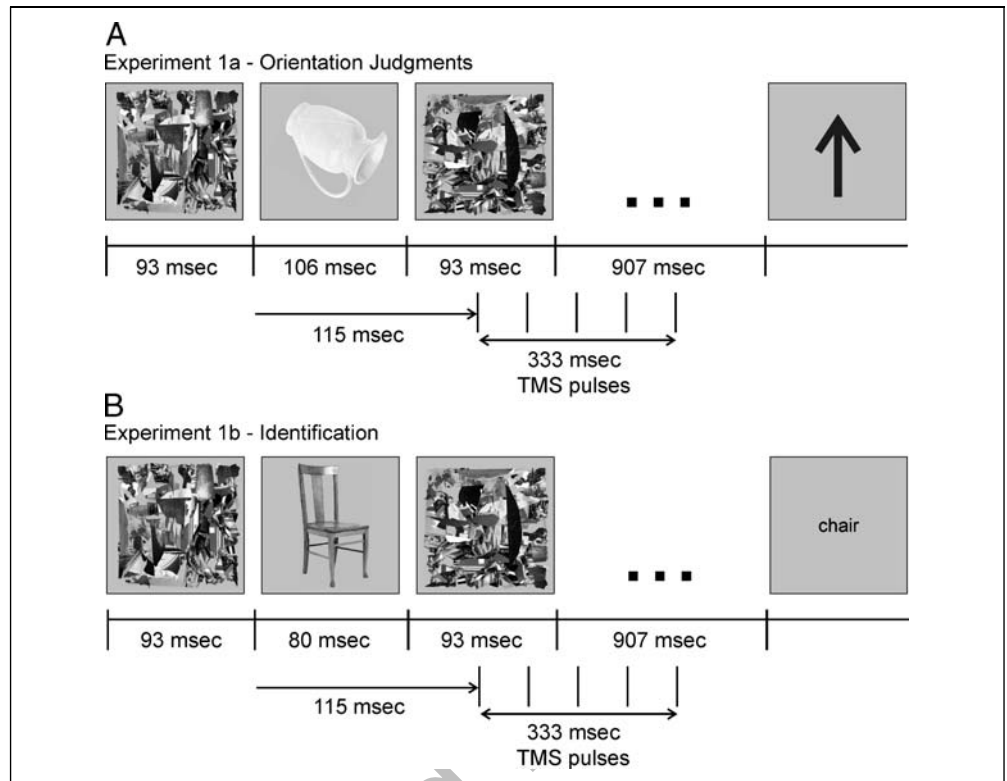
The aim of the present study was to investigate the causal role played by the right parietal lobe in these two processes: the ability to interpret object orientation and the recognition of rotated objects. In order to do this, we used transcranial magnetic stimulation (TMS) to interfere with cortical activity in the right parietal cortex while subjects performed either orientation judgment tasks or identification tasks. In Experiment 1, subjects saw pictures of upright or picture-plane rotated objects that were followed by either an arrow (Experiment 1a, orientation task) or a word (Experiment 1b, identification task) which matched the objects on the required dimension or not (see Figure 1). In Experiment 2, subjects saw a rotated object and either judged its orientation (is it rotated clockwise or counterclockwise?) or its identity (is it "natural" or "manufactured"?). Based on previous imaging and lesion evidence, we targeted a cortical site overlying the posterior and inferior aspect of the IPS, corresponding to the P4 location on the International 10–20 EEG system (see Figure 2). If the right parietal cortex plays a critical role in orientation processing, as suggested by the cases of orientation agnosia, then we would expect TMS to impair orientation judgments. Similarly, if this area is critical for the recognition of rotated objects, then TMS should impair identification when objects are presented in noncanonical orientations. In addition, Experiment 2 also manipulated the time window during which TMS was delivered, in order to delineate the temporal dynamics of the right parietal lobe involvement in these two tasks.

METHODS

Participants

A total of 45 neurologically normal native Italian speakers (27 women), 19 to 44 years old (mean = 27 years), participated in the study. Twelve subjects took part in each of Experiments 1a and 1b; three subjects did both experiments, which were conducted approximately 4 months apart. Twenty-four subjects participated in Experiment 2 (12 in each of Experiments 2a and 2b). All subjects gave informed consent and the experimental protocol was approved by the Ethics Committee of IRCCS Centro San Giovanni di Dio—FBF, Brescia, Italy.

Figure 1. Experiment 1 paradigm. (A) In each trial of Experiment 1a, pictures of objects were presented either in the upright orientation or rotated by 120° (as depicted here). The object was displayed for 106 msec and sandwiched between forward and backward masks. 1 sec later, an arrow was presented for 500 msec and the subject decided whether the orientation of the arrow matched that of the object. A train of five TMS pulses (12 Hz) was delivered starting 115 msec after the onset of the object picture. (B) Experiment 1b followed the same procedure, except that here, subjects had to decide whether a word presented for 500 msec, 1 sec after the object, identified the object. The object was displayed for only 80 msec in the latter experiment. The object name is depicted in English here, but was presented in Italian in the actual experiment.



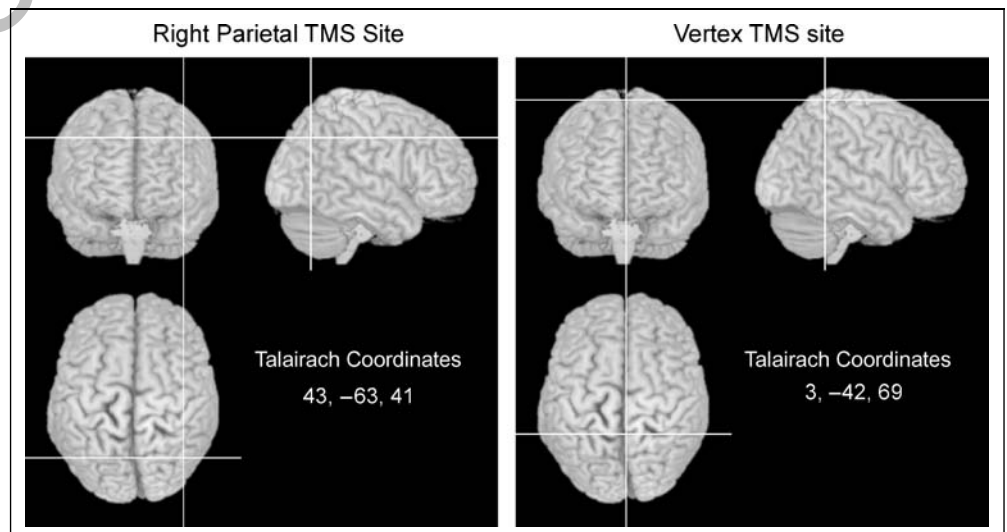
Stimuli and Apparatus

The stimuli were photographs of real objects with a well-defined canonical upright orientation, taken from the Hemera Photo-Object database (Hemera Technologies, Canada). They were converted to gray scale and displayed against a mid-gray background (RGB values: 190, 190, 190). All objects were scaled to 472 pixels in the longest dimension and were viewed from a distance of 80 cm. Four pattern masks were created from collages of

(unrecognizable) fragments of a number of the original pictures, cut into random shapes and superimposed in random orientations.

Stimulus presentation and TMS delivery were controlled by the Presentation software (Neurobehavioral Systems, www.neuro-bs.com) running on a PC. Stimuli were presented on a 17-in. CRT monitor (1024 × 768 resolution) with 75 Hz vertical refresh rate and responses were recorded via the keyboard. Throughout

Figure 2. Stimulation sites. TMS was applied to a right parietal site overlying the posterior and inferior part of the intraparietal sulcus (left panel) or to a control stimulation site at the vertex of the head (right panel).



the experiment, the subject's head was stabilized with a combination of a chin rest and adjustable forehead supports. The TMS coil was fixed in position with the aid of an articulated mechanical arm.

TMS Protocol

TMS was applied using a Magstim SuperRapid stimulator (Magstim, Withland, UK) and a figure-of-eight double 70-mm coil, which can induce a maximum magnetic field of 2.2 Tesla at the scalp site. Before the experiment, individual motor thresholds were determined by stimulating the left motor cortex and observing contractions evoked by a single TMS pulse in the contralateral first interosseus dorsalis muscle. The threshold was defined as the minimum intensity which induced a visible contraction in the tested muscle on at least three trials out of five, when applied over the motor cortex "hot-spot." The stimulation intensity used during the experiment was set at 110% of each subject's threshold. The mean stimulation intensity was 59%, 64%, 63%, and 55% of the maximum output of the TMS coil in Experiments 1a, 1b, 2a, and 2b, respectively.

The subjects wore a close-fitting Lycra skullcap with the electrode locations from the International 10–20 EEG system marked on. The cap was positioned such that the Cz marking corresponded to the individual's measured Cz, thus ensuring that the position of the reference points was constant across subjects. For the right parietal condition, the coil was positioned tangential to the scalp with the handle pointing forward parallel to the long axis of the temporal lobe and the virtual cathode overlying P4. For the vertex condition, the coil was positioned approximately parallel to the floor, with the handle pointing back and the virtual cathode overlying a site 2 cm behind Cz. This stimulation condition reproduced the scalp sensation and the noise associated with the discharge of the coil, but because of the orientation of the coil and the shape of the skull at this location, only a negligible amount of stimulation is likely to have reached the brain, thus acting effectively as a sham condition.

The location of the stimulation sites on the cerebral cortex was estimated using a 3D Fastrack Polhemus digitizer (Polhemus, Colchester, VT) combined with the SofTactic Navigator 3.0 software (EMS, Bologna, Italy). The Fastrack digitizer has four receivers and one stylus (Static Accuracy: 0.03 inches RMS for the x , y , or z position; 0.15° RMS for receiver orientation; Resolution 0.0002 inches per inch of transmitter and receiver separation; 0.025° orientation). Three receivers were placed on the subject's head by means of a dedicated helmet to prevent inaccuracy due to head movements, whereas the fourth receiver was placed onto the TMS coil to measure its position in x , y , and z Cartesian coordinates and orientation (azimuth, elevation, and roll) at the desired stimulation site. Craniometric landmarks

(e.g., nasion, inion, peri-auricular points), along with about 40 other points, were registered on the subject's skull with the stylus. These points were then used by the navigation software to compute an estimated brain volume in Talairach space, by means of a warping procedure applied to a generic MRI volume (the Montreal Neurological Institute template). The precision of this neuronavigation method is within millimeters (Bastings et al., 1998) and is comparable to the spatial resolution of the TMS at motor threshold intensity (Herwig et al., 2001). Talairach coordinates for the stimulation sites (the P4 and the vertex locations described above) were estimated in a group of five individuals and their mean location is pictured in Figure 2.

Experimental Procedures

Experiments 1a and 1b

These two experiments followed the same general procedure. Subjects sat at a table in a dimly lit room, at a distance of 80 cm from the computer monitor. After establishing stimulation thresholds and before commencing the experiment proper, subjects completed 10 practice trials using different objects to those used in the experiment. During the practice, the TMS coil was placed over each stimulation site and trains of TMS pulses were delivered with the same intensity and timing as in the subsequent experimental trials, in order to accustom the subject to the scalp sensation and the noise produced by the stimulator. Following practice, the TMS coil was fixed in position at the relevant site and the subject completed two blocks of 80 trials, one with TMS to the right parietal lobe and one with TMS to a vertex control site, with the order counterbalanced across subjects. Each block was divided into four groups of 20 trials with a fixed inter-trial interval of 7 sec, with short rest breaks allowed after every 20 trials. The experimenter repositioned the coil over the next stimulation site between the two blocks of trials.

Subjects were instructed to respond as accurately and as quickly as possible (accuracy was emphasized over speed) by pressing one of the two Alt keys on the keyboard using the index fingers of both hands. Half the subjects pressed the left Alt key for a "match" response and the right Alt key for a "mismatch" response, whereas the other half responded in the reverse manner.

Both experiments used identical $2 \times 2 \times 2$ within-subject designs. The independent variables were *stimulation site*: right parietal lobe versus vertex; *object orientation*: upright (0°) versus rotated by 120° (half of these were rotated clockwise and half counterclockwise); and *trial type*: match versus mismatch. On each of the 160 trials, the subject saw a different object, with the assignment of stimuli to the eight design cells counterbalanced across subjects. Stimulation site was blocked, with the order of the other two conditions randomly intermixed within these blocks.

Experiment 1a: Orientation Judgment

Subjects were required to judge the orientation of a briefly flashed and masked object (see Figure 1A). Each trial began with a fixation cross for 1 sec, followed by the object sandwiched between a forward and a backward mask. The masks were chosen randomly by the computer on each trial. The object itself was presented for 106 msec and each of the masks for 93 msec. An arrow was presented 1 sec after the offset of the object, for 500 msec, and was followed by a blank screen until the end of the 7-sec-long trial. The subject's task was to decide whether the orientation of the arrow matched that of the object. The arrow could point in one of eight orientations (0° , $\pm 60^\circ$, $\pm 90^\circ$, $\pm 120^\circ$, 180°), whereas the object could be either upright or rotated by $\pm 120^\circ$. In half the trials, the orientation matched that of the object, whereas in the other half, it did not.

A train of five TMS pulses with a frequency of 12 Hz was delivered starting 115 msec after the onset of the object picture, to either the right parietal or the vertex stimulation site.

Experiment 1b: Object Identification

Subjects were required to identify a briefly presented masked object. The trial structure was identical to that of Experiment 1a, with the following exceptions. The object was presented for only 80 msec (because object identification is generally an easier task than orientation judgment) and the arrow was replaced by a word, which was either the name of the object or another concrete noun (see Figure 1B). The subject's task was to decide whether the word matched the object or not. Half the trials were matches and the other half were mismatches.

Experiments 2a and 2b

In these experiments, subjects were required to make a two-alternative, forced-choice (2AFC) decision either about the orientation of an object (Experiment 2a) or about its identity (Experiment 2b) and were instructed to respond as accurately and as quickly as possible. Similar to Experiment 1, each trial began with a fixation cross for 1 sec, followed by an object sandwiched between a forward and a backward pattern mask. The masks were presented for 93 msec each, while the object was presented for either 106 or 118 msec (half the subjects in each experiment saw the object for each duration. There was no difference in performance between durations, so the results were collapsed across exposure duration for the analysis). This was followed by a blank screen until the end of the 7-sec-long trial.

The stimuli were 48 pictures of "natural" objects (e.g., animals, plants, fruit) and 48 pictures of "manufactured" objects (e.g., vehicles, appliances, clothing), all with an unambiguous canonical upright orientation. The objects

could appear in one of six different orientations: $\pm 60^\circ$, $\pm 90^\circ$ and $\pm 120^\circ$ from the upright. The 96 objects were divided such that 8 objects from each category (natural vs. manufactured) were presented in each of the six orientations. The assignment of particular objects to orientations was counterbalanced across versions of the experiment. In Experiment 2a, subjects decided whether the object was tilted clockwise or counterclockwise from its usual orientation. In Experiment 2b, they decided whether it was "natural" or "manufactured." All subjects responded in the same fashion by pressing one of two buttons on the keyboard with two fingers of their right hand (left arrow for "counterclockwise" and "natural" and right arrow for "clockwise" and "manufactured"). The response keys were not counterbalanced because it would have been counterintuitive for subjects to press the left arrow for "clockwise" and the right arrow for "counterclockwise."

For each experiment, two independent variables were manipulated in a 2×2 within-subject design: *stimulation site* (right parietal vs. vertex) and *timing of TMS* (early vs. late), with the four conditions administered in separate blocks of trials. The order of the conditions was counterbalanced across subjects with the restriction that the two blocks at each stimulation site were kept together so the coil was only moved once during the experiment. In the early TMS trials, a train of five TMS pulses (12 Hz frequency) was delivered starting 80 msec after the onset of the object (thus covering a time window 80–413 msec poststimulus), whereas in the late TMS trials, the train of TMS pulses was delivered starting 450 msec after the onset of the object (covering the 450–783 msec time window). These particular time windows were chosen because 80 msec was the earliest time when visual information was likely to reach the parietal lobe (Bar et al., 2006; Schmolesky et al., 1998), thus representing the earliest time at which we might expect to see an effect. The later time window was the subsequent nonoverlapping period of time. All other procedural details were identical to Experiment 1.

RESULTS

Experiment 1

The data from match and mismatch trials were combined to provide an overall measure of accuracy and RT (see Table 1). Figure 3 shows the percentage of correct responses and mean RTs on the correct trials for orientation judgments (left panels) and object identification (right panels) in Experiment 1, plotted as a function of *stimulation site* (right parietal vs. vertex) and *object orientation* (0° vs. 120°). Both accuracy and RT data were analyzed using 2×2 repeated-measures ANOVAs with *stimulation site* and *object orientation* as factors and planned pairwise comparisons between right parietal and vertex stimulation for each object orientation.

Table 1. Mean RT and Percent Accuracy Values

	<i>Right Parietal TMS</i>	<i>Vertex TMS</i>
	<i>RT (% Correct)</i>	<i>RT (% Correct)</i>
<i>Experiment 1a: Orientation Judgment</i>		
Upright objects	874 (82)	852 (90)
Rotated objects	1005 (61)	1048 (67)
<i>Experiment 1b: Object Identification</i>		
Upright objects	913 (84)	931 (80)
Rotated objects	1019 (77)	1047 (70)
<i>Experiment 2a: Orientation Judgment</i>		
Early stimulation	1022 (60)	1019 (69)
Late stimulation	1031 (62)	1089 (69)
<i>Experiment 2b: Object Identification</i>		
Early stimulation	944 (79)	1064 (83)
Late stimulation	938 (81)	998 (84)

Experiment 1a: Orientation Judgment

Accuracy. Subjects were generally more accurate with upright compared to rotated objects [$F(1, 11) = 60.20, p < .001$] (see Figure 3A). TMS to the right parietal lobe reduced accuracy compared to TMS administered over the vertex control site [$F(1, 11) = 6.22, p = .030$] and there was no interaction between stimulation site and object orientation [$F(1, 11) = 0.08, p = .78$]. Planned comparisons between right parietal and vertex stimulation indicated marginally significant differences in both the upright and the rotated stimulus conditions [$t(11) = 2.06, p = .064$ and $t(11) = 2.03, p = .068$, respectively]. Thus, it appears that right parietal stimulation reduces the ability to interpret the orientation of objects, both when the object is in its canonical orientation (8% reduction in accuracy) and when it is rotated away from the upright (6% reduction in accuracy).

Reaction times. As can be seen in Figure 3C, RTs were generally slower for rotated objects compared to upright objects [$F(1, 11) = 15.72, p = .002$], but there was no discernable effect of stimulation site on RTs [$F(1, 11) = 0.042, p = .84$], nor was there an interaction between stimulation site and object orientation [$F(1, 11) = 3.20, p = .10$]. Planned comparisons between right parietal and vertex stimulation showed no differences for either upright or rotated stimuli ($ts < 0.82, ps > .43$). This is probably due to the difficulty of the task, which required the evaluation of a very briefly displayed and heavily masked object; under such conditions, subjects find it

quite challenging to form a lasting impression of the object and make a decision and, therefore, any potential differences in RT tend to be obscured by ceiling effects.

Speed–accuracy tradeoffs. Inspection of Figure 3A and C raises the possibility of a speed–accuracy tradeoff in the case of rotated objects, with accuracy being lower and RT somewhat faster in the right parietal TMS condition compared to the vertex condition. To verify this, we calculated difference scores based on each subject’s performance with rotated objects by subtracting each individual’s mean performance in the right parietal TMS condition from their mean performance in the vertex stimulation condition, for both accuracy ($M_{\text{AccVertex}} - M_{\text{AccRightParietal}}$) and RT ($M_{\text{RTVertex}} - M_{\text{RTRightParietal}}$). There was no correlation between accuracy and RT difference scores, $r = .08, ns$, indicating that there was no systematic tradeoff between speed and accuracy.

Experiment 1b: Object Identification

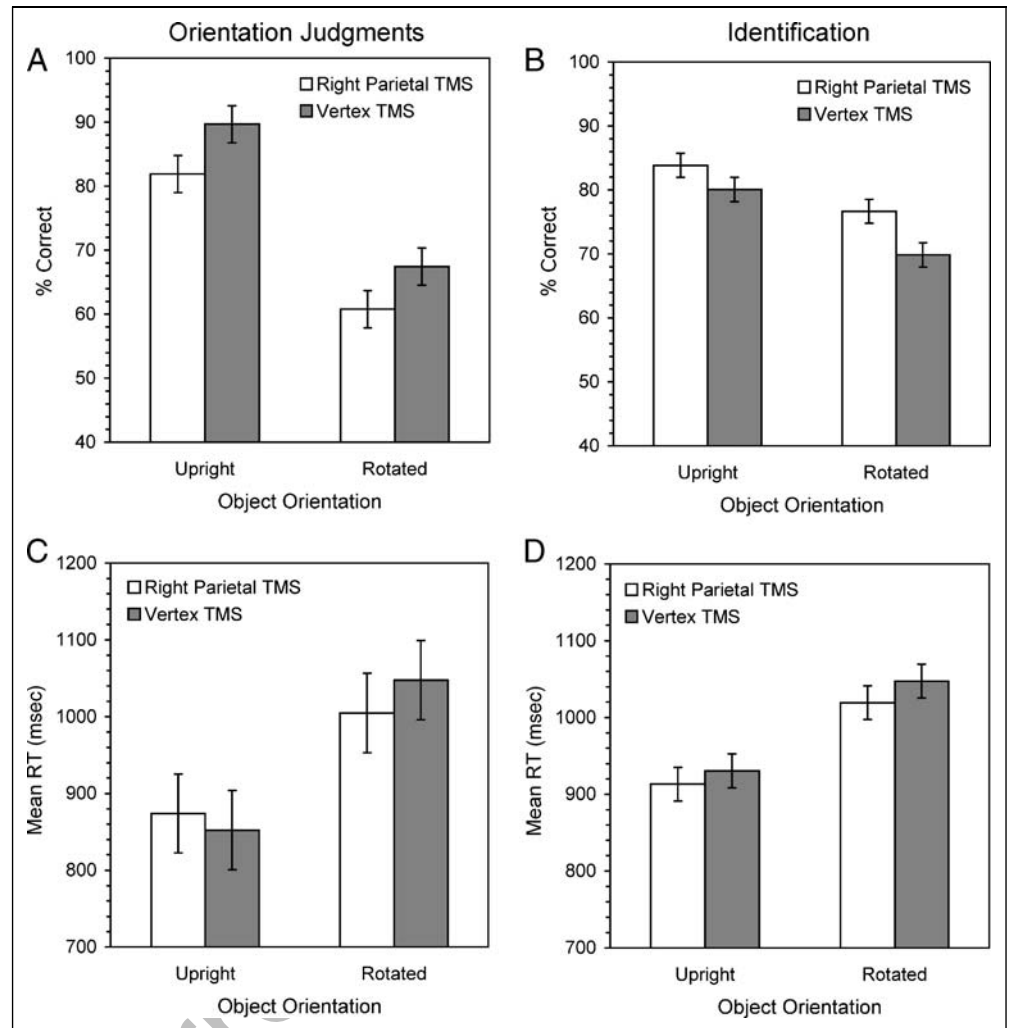
Accuracy. As one might expect, subjects were less accurate at identifying rotated objects compared to upright objects [$F(1, 11) = 32.53, p < .001$]. Interestingly, TMS affected object identification in a completely different way to its effects on orientation judgments (see Figure 3B)—that is, TMS to the right parietal lobe *improved* identification accuracy compared to TMS to the vertex site [$F(1, 11) = 7.86, p = .017$]. Although the ANOVA interaction term failed to reach significance [$F(1, 11) = 1.75, p = .213$], Figure 3B suggests that this improvement was numerically greater for rotated objects (7%) than for upright objects (4%). This was confirmed by planned comparisons, which indicated that the improvement in accuracy was significant for rotated objects [$t(11) = 3.49, p = .005$], but not for upright objects [$t(11) = 1.54, p = .15$].

Reaction times. Subjects were again slower overall with rotated objects than with upright objects [$F(1, 11) = 32.01, p < .001$]. However, there was no effect of stimulation site [$F(1, 11) = 1.07, p = .32$], and no interaction between stimulation site and orientation [$F(1, 11) = 0.11, p = .75$]. Planned comparisons between right parietal and vertex stimulation showed no differences, for either upright or rotated stimuli ($ts < 0.96, ps > .36$). Thus, similar to Experiment 1a, TMS did not have an effect on RT.

Experiment 2

Figure 4 shows the percentage of correct responses and mean RT on correct trials for the orientation judgments (left panels) and object identification (right panels) in Experiment 2, plotted as a function of *stimulation site* (right parietal vs. vertex) and *timing of TMS* (early vs. late). Both accuracy rates and RTs were analyzed using 2×2 repeated-measures ANOVAs with stimulation site and timing of TMS as factors and planned pairwise

Figure 3. Results of Experiment 1. Mean accuracy (top) and mean reaction times (bottom) for orientation judgments (left) and object identification (right), plotted separately for upright and rotated objects. The white bars represent the right parietal TMS condition and the black bars the vertex TMS condition. Error bars represent within-subject *SEM* for the TMS effect.



comparisons between right parietal and vertex stimulation in each time window.

Experiment 2a: Orientation Judgments

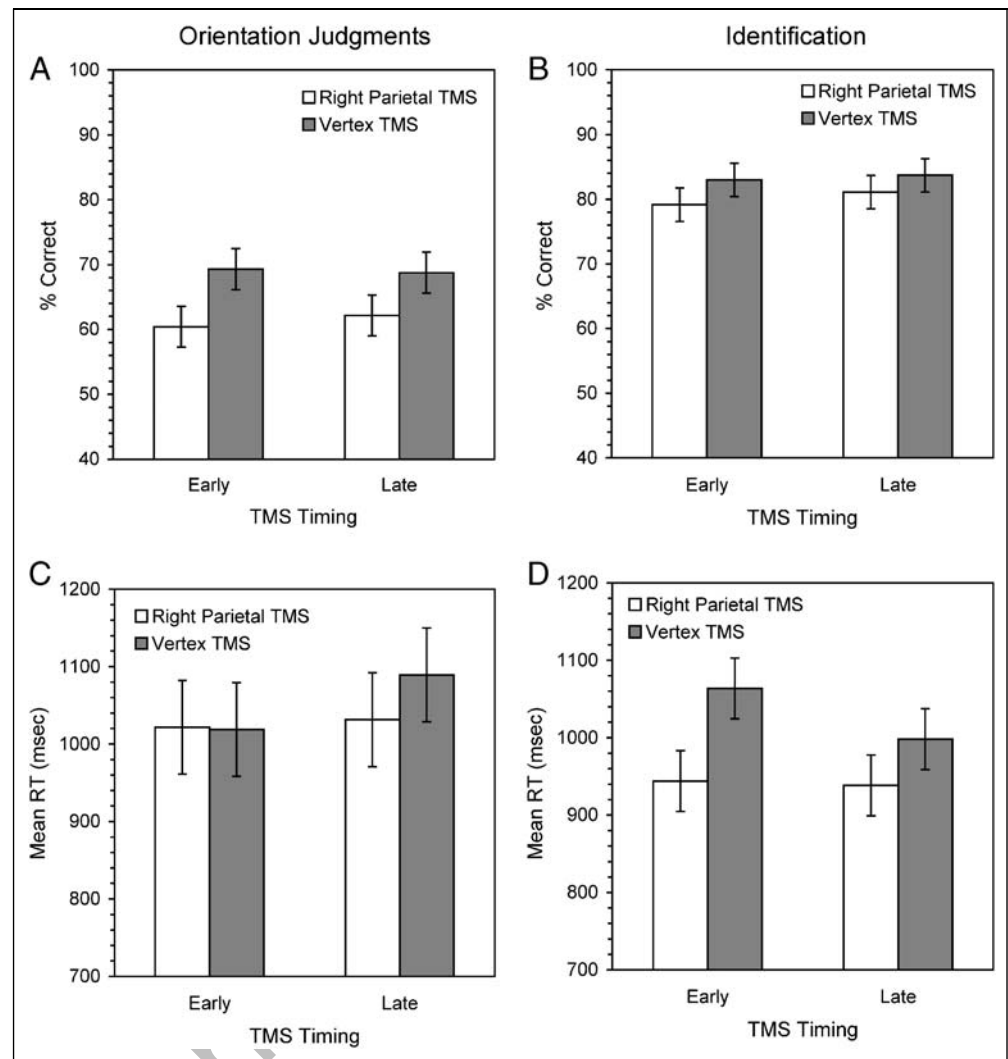
Accuracy. TMS to the right parietal lobe reduced overall accuracy of orientation judgments compared to TMS to the vertex site [$F(1, 11) = 5.99, p = .032$]. There was no main effect of timing [$F(1, 11) = 0.03, p = .859$] and no interaction between timing of TMS and stimulation site [$F(1, 11) = 0.14, p = .71$]. Individual planned comparisons between right parietal and vertex stimulation fell short of significance both in the early and late stimulation window [$t(11) = 1.98, p = .073$ and $t(11) = 1.57, p = .15$, respectively]. Moreover, the reduction in accuracy was of similar size when TMS was applied in the early (9% reduction) and in the late time window (7% reduction). This suggests that the involvement of the right parietal lobe in orientation judgments is not confined to either one of the stimulation time windows tested here. It is possible that the involvement of the right parietal lobe in orientation judgments spans the entire time

window sampled, between 80 and 783 msec, or that its involvement is restricted to a smaller time window that straddles both the early and late periods sampled here; the present results cannot distinguish between these two possibilities.

Reaction times. There was no overall effect of stimulation site on RTs [$F(1, 11) = 0.21, p = .66$], no difference between early and late stimulation [$F(1, 11) = 0.79, p = .39$], and no interaction between these factors [$F(1, 11) = 1.22, p = .29$]. This was confirmed by planned comparisons between right parietal and vertex stimulation in each time window ($ts < 0.82, ps > .43$).

Speed-accuracy tradeoffs. The data in Figure 4C again suggested the possibility of a speed-accuracy tradeoff in the late TMS time window, but this was disconfirmed by a correlation analysis of RT and accuracy difference scores between right parietal and vertex TMS conditions (calculated as in Experiment 1a). This analysis initially yielded a near-significant *negative* correlation, $r = -.548, p = .065$, which is the opposite of a speed-accuracy tradeoff (i.e., a smaller accuracy impairment was accompanied by a greater speeding up of RT).

Figure 4. Results of Experiment 2. Mean accuracy (top) and mean reaction times (bottom) for orientation judgments (left) and object identification (right), plotted separately for early and late stimulation time windows. The white bars represent the right parietal TMS condition and the black bars the vertex TMS condition. Error bars represent within-subject *SEM* for the TMS effect.



However, inspection of individual subjects' performance revealed that this effect was entirely driven by one subject who had an extremely large RT difference (516 msec) between the right parietal and vertex TMS conditions; when this subject was excluded from the analysis, any correlation between accuracy and RT disappeared, $r = .18$, *ns*.

Experiment 2b: Object Identification

Accuracy. TMS did not affect identification accuracy [$F(1, 11) = 1.54$, $p = .24$]. Similarly, there was no overall effect of timing of TMS [$F(1, 11) = 0.20$, $p = .66$] or interaction between timing of TMS and stimulation site [$F(1, 11) = 0.05$, $p = .82$]. Planned comparisons between right parietal and vertex stimulation in each time window likewise failed to find any significant differences in identification accuracy ($t_s < 1.07$, $p_s > .31$).

Reaction times. Right parietal TMS resulted in significantly faster RTs than TMS to the vertex [$F(1, 11) =$

5.23 , $p = .043$] and there was no main effect of timing of TMS [$F(1, 11) = 0.38$, $p = .551$]. Planned comparisons between right parietal and vertex stimulation confirmed that the facilitation in RT was marginally significant in each of the time windows [$t(11) = 1.96$, $p = .076$ and $t(11) = 2.07$, $p = .063$, for the early and late TMS, respectively]. Figure 4D suggests that the facilitation effect following right parietal stimulation was larger when TMS was applied in the early time window than when it was applied late—a reduction of 120 msec versus 60 msec—but the interaction between stimulation site and timing of TMS was not significant [$F(1, 11) = 1.20$, $p = .29$]. Inspection of individual subjects' data revealed that the apparently larger facilitation effect in the early time window was due to one subject who showed a very large difference (600 msec) between early and late vertex stimulation conditions. When this subject's data are excluded, the RT facilitation in the early time window is smaller (86 msec, as opposed to 120 msec), and closer to the size of the facilitation effect in the late time window (56 msec).

Speed-accuracy tradeoffs. Figure 4B and D suggests a potential speed-accuracy tradeoff in this experiment, in that right parietal stimulation resulted in significantly faster RTs and somewhat lower (although not significantly so) accuracy compared to vertex stimulation. To verify this, we calculated difference scores between right parietal and vertex stimulation for each subject's overall mean accuracy ($M_{AccVertex} - M_{AccRightParietal}$) and overall mean RT ($M_{RTVertex} - M_{RTRightParietal}$) and found them to be uncorrelated, $r = .13, p = .68$. This was also the case when the correlations were performed separately for the early and late time windows ($r_s < .44, p_s > .15$).

DISCUSSION

This study investigated the effects of TMS applied to a right parietal site overlying the inferior parietal lobe/IPS while subjects performed orientation judgment or identification tasks involving upright and rotated objects. If this area is critically involved in these two processes, then there is no reason to expect different patterns of results on the two tasks; in both cases, we should see impairments in performance caused by stimulation to the right parietal lobe. This is not what we found. Right parietal TMS impaired orientation judgments, but facilitated object identification, compared to stimulation at a vertex control site.

Experiment 1a demonstrated that brief (333 msec) interference with cortical activity in the right parietal lobe during an orientation matching task impaired subjects' accuracy in judging object orientation. This reduction in accuracy was of similar magnitude for upright and rotated objects (6% and 8%, respectively). Experiment 2a confirmed this finding and further showed that the impairment in orientation judgments was present, in equal measure, in the early and late time windows of stimulation (7% and 9% reduction, respectively). Thus, the results of Experiments 1a and 2a demonstrate that the right IPS/inferior parietal lobe is a necessary neural substrate for processing the spatial orientation of objects, consistent with findings from patients with object orientation agnosia (Harris et al., 2001; Turnbull et al., 1997).

In sharp contrast, TMS applied to the same region of the right parietal lobe led to an *improvement* in object identification, compared to the vertex control stimulation. This was reflected in better response accuracy in Experiment 1b and faster RTs in Experiment 2b. In Experiment 1b, there was somewhat greater improvement in identification of rotated objects (7%) than of upright objects (4%). Although this may be due to a ceiling effect in the case of upright objects, it could also indicate that the right parietal lobe plays a more important role in the identification of rotated, compared to upright, objects. Experiment 2b also yielded a facilitatory effect of right parietal TMS on identification of rotated objects, although here the effect was expressed as a reduction in

RT rather than an improvement in accuracy rates. This facilitation was seen both in the early and late stimulation windows in roughly equal measure. In sum, across different paradigms, we see this facilitation reflected in a variety of performance measures.

One possible explanation for the apparent facilitation in object identification following right parietal TMS is that it results from an actual impairment in performance during the vertex stimulation condition used as a baseline here. On the face of it, the vertex site chosen in this study is not near any known object or space-processing related brain areas, which makes this proposal quite unlikely. However, it is conceivable that stimulation at the vertex site may have interfered with interhemispheric communication via the corpus callosum and some models of object recognition suggest that such hemispheric cross-talk is crucial for semantic categorization and identification of objects seen from unusual views (Warrington & Taylor, 1978). We do not think that this is a likely scenario, for two reasons. First, the corpus callosum is a distance of some 4 to 5 cm from the surface of the skull, which probably puts it outside the range of effective stimulation, due to the rapid fall-off of the magnetic field strength at greater penetration depth. Second, one would expect that the interhemispheric fibers connecting the perceptual brain areas involved in object processing would be in the more posterior part of the corpus callosum and, thus, even further from the site of stimulation. Thus, we would argue that the results obtained here indicate a genuine facilitation effect of right parietal stimulation rather than an impairment caused by stimulation to the vertex site.

Facilitation effects of TMS are sometimes demonstrated in cognitive tasks and could, in principle, be interpreted as evidence that the stimulated brain region is critical for performing the task under investigation and that TMS improves processing efficiency by increasing cortical excitability. However, it seems highly unlikely, in our case, that TMS during identification tasks could have somehow improved processing efficacy in the right parietal lobe, given that the same stimulation parameters produced a clear-cut disruption in orientation judgments. For this reason, we would maintain that TMS disrupted cortical processing in the parietal lobe during the identification task as well. Therefore, we conclude that the pattern of results obtained in Experiments 1b and 2b does *not* support the notion that the right parietal lobe is necessary for object identification per se.

The fact that we did find an effect (albeit one of facilitation) of right parietal TMS on object identification does, however, suggest that activity in this region impinges on the recognition process in some way. For example, it is possible that TMS interferes with long-range inhibitory projections from the parietal lobe to some other area involved in object recognition, such as the ventral stream, or to areas involved in response selection and execution, such as the prefrontal and/or

motor cortex. The net effect of suppressing parietal activity, therefore, would be to remove this inhibition and facilitate task performance. The present results suggest that this facilitation is more pronounced when dealing with rotated rather than upright objects, which suggests a more specific effect than merely a general inhibitory connection with object identification or response selection areas. So, how could we account for the functional role of the right parietal lobe in object identification?

A Role for the Right Parietal Lobe in Object Consolidation?

As mentioned in the Introduction, previous experiments that used brief object presentations suggest that there are two stages involved in object recognition. The first is a preliminary recognition stage in which the identity of the object is activated through orientation-invariant representations and which is generally completed within the first 100 msec of stimulus processing. The second is a consolidation stage in which the object identity is placed in a spatial reference frame, thereby allowing one to interact with the object and to individuate specific visual instances of the object (Dux & Harris, 2007; Harris & Dux, 2005a). Dux and Harris (2007) have shown that the performance costs often elicited when subjects identify rotated objects arise during this consolidation stage and that they appear to be due to a need to reconcile the orientation cues extracted from the visual stimulus with the expected (i.e., canonical) orientation retrieved from memory along with the object's identity (see also Harris & Dux, 2005b). This process can delay the consolidation of rotated objects, often precluding stimulus detection under time-constrained conditions as, for example, in Experiment 1b, where subjects were significantly less likely to identify rotated objects compared to upright ones in the short time available for processing the stimulus.

Given the important role of the right parietal lobe in processing object orientation demonstrated in Experiments 1a and 2a, along with its more general role in spatial imagery and spatial transformation (Sack, Camprodon, Pascual-Leone, & Goebel, 2005; Harris & Miniussi, 2003; Sack et al., 2002), it seems reasonable to propose that this brain area is involved in this consolidation stage of object recognition. Thus, if TMS disrupts the ability to code the spatial orientation of the stimulus, this could have the effect of removing the need to reconcile conflicting spatial reference frames and would speed up the consolidation of the object's identity in a reportable form. Although we do not wish to make a strong claim about this, it may be significant that the size of the TMS effect on accuracy was about the same magnitude in both tasks—the accuracy of judging orientation went down by ~7% and the accuracy of identifying rotated objects went up by 7%. This would be consistent with the idea

that the contribution of the right parietal lobe to these two processes is somewhat complementary.

Clinical Implications

The findings of this study essentially mimic the cardinal symptoms of object orientation agnosia. We found that disrupting cortical activity in the right parietal lobe impaired the ability to judge the orientation of objects, left recognition of rotated objects intact (and even improved it), and diminished the RT costs usually associated with identifying rotated objects. Therefore, these results provide strong evidence that the critical lesion in this syndrome is localized to the right IPS/inferior parietal lobe.

The relation between our results and the syndrome of apperceptive agnosia is less clear. We did not find any evidence of object recognition impairments following TMS to the parietal lobe, but this may have happened for a number of reasons. First, it is possible that the critical lesion that gives rise to apperceptive agnosia is located in a somewhat different brain region, which was not reached by TMS in our experiments. Second, the “unusual-views” recognition deficit that characterizes apperceptive agnosia has typically been demonstrated using depth-rotated or severely foreshortened views of objects (e.g., a bucket seen from above). Although rotations in the picture-plane can also be considered in some sense “unusual” (Turnbull & McCarthy, 1996), most apperceptive agnosics have not been tested with picture-plane rotated objects. We used picture-plane rotations in this study because they are the best stimuli for dissociating object shape and orientation without altering other aspects of the stimulus, such as the presence of features and object geometry. However, it may be that right parietal lesions/TMS affect recognition of depth-rotated and picture-plane-rotated objects in different ways. These issues remain to be addressed in future studies. Nonetheless, the present results do provide tentative support for the notion that apperceptive agnosia following right parietal lesions may reflect spatial processing impairments (such as not being able to determine which view of an object one is looking at), rather than a pure disorder of object recognition (Warrington & James, 1988).

Conclusions

We have shown that TMS applied to the IPS/inferior parietal lobe of the right hemisphere impairs the ability to judge the orientation of objects, while at the same time facilitating recognition of the same objects. This pattern of results offers support to the notion that the parietal lobe—a dorsal stream region—is critical for processing the spatial attributes of objects, but not their identity. At the same time, however, our results are consistent with an indirect role for this area in object recognition, which

involves consolidating the identity of the object in a spatial reference frame, thereby allowing interaction with the object and individuation of different visual instances of it. As such, these results also speak to the importance of cross-talk between the two visual streams in object processing and perceptual awareness.

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