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Transcranial magnetic stimulation over MT/MST fails to impair judgments of implied motion

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The medial temporal and medial superior temporal cortex (MT/MST) is involved in the processing of visual motion, and fMRI experiments indicate that there is greater activation when subjects view static images that imply motion than when they view images that do not imply motion at all. We applied transcranial magnetic stimulation (TMS) to MT/MST in order to assess the functional necessity of this region for the processing of implied motion represented in static images. Area MT/MST was localized by the use of a TMS-induced misperception of visual motion, and its location was verified through the monitored completion of a motion discrimination task. We controlled for possible impairments in general visual processing by having subjects perform an object categorization task with and without TMS. Although MT/MST stimulation impaired performance in a motion discrimination task (and vertex stimulation did not), there was no difference in performance between the two forms of stimulation in the implied motion discrimination task. MT/MST stimulation did, however, improve subjects' performance in the object categorization task. These results indicate that, within 150 msec of stimulus presentation, MT/MST is not directly involved in the visual processing of static images in which motion is implied. The results do, however, confirm previous findings that disruption of MT/MST may improve efficiency in more ventral visual processing streams.

Many objects in the world are not static but are constantly moving. Thus, it is not surprising that certain regions of the brain seem to be specialized for the task of processing motion. Neurons in the medial temporal and medial superior temporal cortex (MT/MST, also known as V5) respond preferentially to visual stimuli that are moving. The sensitivity of these neurons to moving stimuli correlates with perceptual judgments about those stimuli (Newsome, Britten, & Movshon, 1989), and electrical stimulation of MT/MST further influences one's perceptual judgments about perceived motion (Salzman, Britten, & Newsome, 1990; Salzman & Newsome, 1994). In humans, both PET and fMRI have shown that MT/MST is sensitive to motion that is defined by spatiotemporal changes in luminance (Tootell, Reppas, Kwong, et al., 1995; Watson et al., 1993), as well as to motion that is defined by "second-order" characteristics, such as contrast modulation (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998). In addition, studies using PET and fMRI have shown that MT/MST is sensitive to illusory contours in motion (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998), apparent motion (Kaneoke, Bundou, Koyama, Suzuki, & Kakigi, 1997), illusory motion produced by either static figures or visual motion aftereffects (Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 2003; Tootell, Reppas, Dale, et al., 1995; Zeki, Watson, & Frackowiak, 1993), and imagined motion (Goebel et al., 1998).

Although these studies focused on the perception of motion (whether real, illusory, or imagined), psychophysical evidence indicates that observers also extract motion-indicative information from images of things or people that are not moving. If motion in an image is strongly implied—as in an image of a person who appears to be jumping from a ledge—subjects are inclined to misremember the event depicted in the photograph as occupying a moment in time later than that actually captured in the photograph, a phenomenon referred to as *representational momentum* (Freyd, 1983). A time shift effect is seen when motion is implied through the viewing of a series of static images (Freyd & Finke, 1984) or by the sudden removal of a supporting structure from the image (Freyd, Pantzer, & Cheng, 1988). This effect is even seen in images that merely imply directionality, such as those of arrows (Freyd & Pantzer, 1995).

Given the psychophysical expectation of motion observed in representational momentum studies and strong MT/MST activation seen in conjunction with the reported perception of motion, a hypothesis can be made that MT/MST activation should be evident when subjects view static images that imply motion. Indeed, there is a significant increase in blood-oxygenation-level-dependent activity in MT/MST when subjects view static images of objects that imply motion in contrast with images of the same object that do not imply motion (Kourtzi & Kanwisher, 2000; Senior et al., 2000). Kourtzi and Kanwisher

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Figure 1. Examples of images used for the implied motion discrimination and object categorization tasks.

argued that this MT/MST activation is due to top-down connections, rather than to the direct involvement of MT/MST in the visual processing of the static image, citing the fact that visual attention has been shown to affect MT/MST activity in both single-unit (Treue & Maunsell, 1999) and fMRI (Beauchamp, Cox, & DeYoe, 1997; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990; Corbetta, Miezin, Shulman, & Petersen, 1991; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997) studies, and that MT/MST activity is greater for imagining moving images than for imagining stationary ones (Goebel et al., 1998).

Thus, although activation is seen in MT/MST when static images that imply motion are viewed, it may still be the case that this activity is superfluous and is not involved in cognitive decisions that relate to the image. That is, the activation may be purely top down in the sense that these images that imply motion lead to motion imagery and may, therefore, be purely incidental to any visual processing of the image. The fMRI results are agnostic with regard to this interpretation. However, the degree of functional involvement of MT/MST in cognitive processing of implied motion can be assessed through the use of transcranial magnetic stimulation (TMS). TMS delivers a brief (1-msec), focused magnetic pulse through the scalp, creating a transient electrical field in the area of cortex underlying the TMS coil. This adds noise to the neural processing for which the stimulated region of cortex is responsible, effectively creating a "virtual lesion" (Lomber & Galuske, 2002). TMS over MT/MST has previously been shown to impair performance in motion discrimination tasks (Beckers & Hömberg, 1992; Beckers & Zeki, 1995; Hotson & Anand, 1999; Hotson, Braun, Herzberg, & Boman, 1994) and disrupt the motion aftereffect illusion (Stewart, Battelli, Walsh, & Cowley, 1999; Théoret, Kobayashi, Ganis, Di Capua, & Pascual-Leone, 2002), as well as the priming of motion direction (Campana, Cowey, & Walsh, 2002).

In addition, TMS over MT/MST has revealed functional competition between cortical regions. When subjects are asked to perform a visual search task, TMS disrupts motion–form conjunction searches but actually enhances color–form conjunction searches (Walsh, Ellison, Battelli, & Cowey, 1998), although these effects seem to depend on subjects' foreknowledge of the upcoming task (Ellison, Battelli, Cowey, & Walsh, 2003). To determine whether MT/MST is involved in the cognitive processing of static images that imply motion (see Figure 1), we hypothesized that TMS over MT/MST would disrupt performance in an implied motion discrimination task. In considering the extent to which an object categorization task relies on the same visual processing pathways that are involved in color–form conjunction searches (Walsh et al., 1998), we further hypothesized that TMS disruption of MT/MST would facilitate ventral stream processing, leading to improved performance in the object categorization task.

METHOD

Subjects

Nine subjects from the University of Oregon community (7 males and 2 females) ranging in age from 18 to 32 years old participated in this experiment. Two subjects were dropped from the experiment: While one subject was being tested, the experiment had to be aborted due to equipment failure; another subject failed to complete the tasks correctly, performing at chance throughout all phases of the experiment. We therefore collected usable data from a total of 7 subjects. Each subject was right-handed, had normal or corrected-to-normal vision, and had no familial history of epilepsy. Subjects were financially compensated for their participation. Subjects signed an informed consent notice that explained the nature of the procedure and the small but potential risks of the application of transcranial magnetic stimulation. The procedures were approved by the University of Oregon Institutional Review Board.

Transcranial Magnetic Stimulation

Subjects' heads were held stationary by means of a chinrest located 40 cm from the computer monitor. Through previous studies, researchers have localized MT/MST at 3–4 cm dorsal from the inion and 4–5 cm lateral from the midline (Ellison et al., 2003; Matthews, Luber, Qian, & Lisanby, 2001; Walsh et al., 1998). After these coordinates were located in individual subjects, a preliminary target region was marked on a nylon swim cap. To further localize MT/MST, we asked subjects to fixate on a random-dot cinematogram at 100% motion coherence. Starting at 50% maximum output, a single pulse was delivered using a Magstim 200 Mono Pulse device with a figure-of-eight coil. Subjects were asked to report whether the pulse caused any disruption to the perception of motion. Verbal descriptions of disruption included "momentary blurring," "dots moved backward," "dots stopped," and "a brief flash," the latter comment suggesting that visual phosphenes were induced. If no perceptual distortion was initially reported, areas within 1 cm of the marked lo-

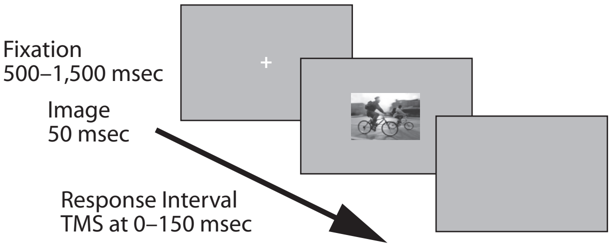

Figure 2. Schematic representation of the experimental paradigm used. TMS, transcranial magnetic stimulation.

cation were tested for an additional 3–4 trials. If none of these pulses resulted in a reported disruption of the perception of motion, output strength was increased by 10%, and the process was repeated. The median pulse strength required to disrupt the perception of motion was 70% of maximum output, with a range from 60% to 80%. These results were comparable with those found in previous research, in which noticeable effects on behavior were reported when a pulse of 70% of maximum was delivered to MT/MST using the same TMS device (Ellison et al., 2003; Walsh et al., 1998). After the subjects had completed a series of practice trials and had situated themselves in the chinrest as comfortably as possible, the coil was positioned tangentially to the skull over MT/MST and was locked in place by means of a clamp. It was stressed to the subjects that they must feel the coil touching their scalps for the duration of the experiment.

Procedure

Data were collected using Presentation on a standard desktop PC in a well-lit room, with stimuli presented on an 18-in. monitor set to a 1,024 × 768 resolution. The experiment was divided into six blocks (three discrimination tasks with stimulation over MT/MST and three with stimulation over vertex, counterbalanced across subjects), with 60 trials per block. For all tasks, subjects were asked to respond as accurately and as quickly as possible. Each trial proceeded as follows (Figure 2): First, a fixation cross was displayed for a variable time from 500 to 1,500 msec, in 500-msec increments. At the end of this interval, visual stimuli appeared and remained onscreen for three screen refreshes (60 Hz), or a total of 50 msec, and TMS pulses were delivered at 0, 50, 100, and 150 msec, relative to stimulus onset, with 12 trials per SOA condition. As a control, TMS was omitted on an additional 12 trials. The order of SOA conditions was randomized within each testing block.

For additional confirmation that MT/MST was being disrupted (beyond verbal report alone), subjects first performed a motion discrimination task. In this control task, a random-dot pattern, with dots at 50% contrast (mean luminance at monitor surface of 6.7 cd/m^2), was displayed at 100% motion coherence within a 6-cm-diameter circle (approximately 8.5º of visual angle) presented at fixation against a black background (luminance at monitor surface of 1.2 cd/m^2). In order to produce the effect of motion, the dot pattern was shifted either to the left or to the right by 2 pixels per screen refresh (approximately 3º/sec). To avoid potential floor effects, the horizontal shift was increased to 4 pixels per screen refresh (approximately 6º/sec) for Subjects 7 and 8 after they claimed that they were unable to perform the task at the slower speed, even without TMS. In the motion discrimination task, subjects were asked to indicate with a mouse-click whether the dots were moving either to the left or to the right (left-click for leftward movement, and right-click for rightward movement). Each trial ended when a response was made, and the computer logged the interval between stimulus presentation and response. If a subject failed to respond within 5 sec, the trial was aborted. Responses made before visual stimulus presentation were not registered, and the trial continued. After the motion task was run at each TMS location, the implied motion discrimination and the object categorization tasks were run, with the order counterbalanced across subjects.

For the implied motion and categorization tasks, stimuli consisted of high-contrast black-and-white images (luminance ranging from 20 to 85 cd/m^2) measuring roughly 9 × 11 cm (approximately 13º × 15.5º of visual angle), presented at fixation. Each photograph depicted either a human or an animal with implied motion either to the left or to the right (Figure 1). Each picture was displayed only once per subject, and photographs were pseudorandomized and counterbalanced for each subject, so that—in the implied motion discrimination task—exactly half the images implying motion to the left were of animals, and the other half were of people; similarly, half the images implying motion to the right were of animals, and the other half were of people. The same counterbalancing procedure was used for the object categorization task. In the implied motion discrimination task, it was irrelevant whether the picture was of an animal or a person, and subjects were asked to indicate with a mouse-click whether the action in the scene was moving either to the left or to the right (left-click for leftward implied movement, and right-click for rightward implied movement). In the object categorization task, the implied motion was irrelevant, and subjects had to indicate whether the briefly presented photograph contained an animal or a person (left-click for animal, right-click for person). Each trial ended when a response was made, and the computer logged the interval between stimulus presentation and response. If a subject failed to respond within 5 sec, the trial was aborted. Responses made before visual stimulus presentation were not registered, and the trial continued.

RESULTS

Control Task

The purpose of the motion task was to statistically verify the verbal reports given by our subjects—that motion processing had been impaired by TMS pulse delivery. Raw response time (RT) and accuracy measurements for the motion discrimination task are displayed in Table 1. To control for within-subjects variability in speed of performance, RTs were normalized within each condition for

Table 1
Mean Response Times (RTs, in Milliseconds; With Standard Errors) and Percent Accuracy (% Acc) for Each Experimental Condition, Across Subjects

	Motion Task						Implied Motion						Object Categorization					
	MT/MST			Vertex			MT/MST			Vertex			MT/MST			Vertex		
SOA	RT			RT			RT			RT			RT			RT		
(msec)	*M*	*SE*	% Acc	*M*	*SE*	% Acc	*M*	*SE*	% Acc	*M*	*SE*	% Acc	*M*	*SE*	% Acc	*M*	*SE*	% Acc
0	749	42	64	711	42	79	653	27	87	709	41	92	668	24	93	777	40	93
50	739	42	82	689	39	81	720	45	88	693	51	88	645	35	95	823	55	91
100	691	36	78	705	40	81	668	31	98	725	57	87	670	29	95	724	50	88
150	690	41	86	657	32	82	628	22	91	704	37	86	700	33	94	764	37	93
None	655	37	83	688	40	81	610	20	91	643	31	93	702	32	99	701	31	90

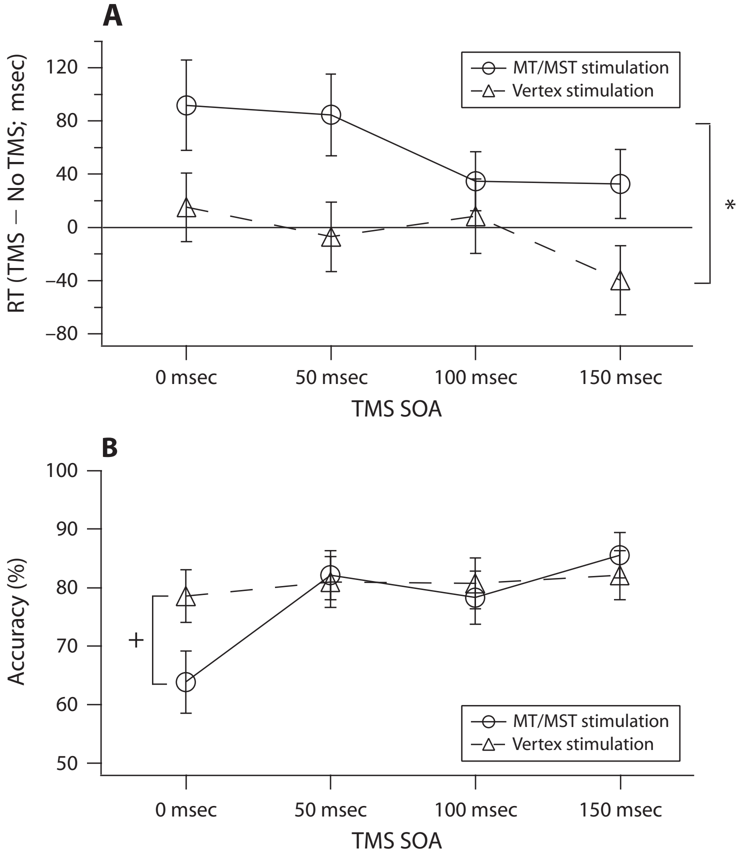

Figure 3. Results from the motion discrimination task used to verify that area MT/MST was targeted. (A) Mean RT differences from the no-transcranial magnetic stimulation (TMS) condition by TMS onset asynchrony for MT/MST and vertex stimulation. Relative to vertex stimulation, MT/MST stimulation produced significantly slower response times, indicating a disruption in motion processing. (B) Mean accuracy × TMS onset asynchrony for MT/MST and vertex stimulation, displaying a significant site by onset asynchrony interaction, primarily due to a reduction of accuracy with MT/MST stimulation at 0 msec. Error bars indicate ±1 standard error of the mean and contain both within-subjects and between-subjects variance. Significance is indicated by (*) *p* < .05 and (+) *p* < .05. (* indicates ANOVA main effect; + indicates independent-samples *t* test.)

each subject by subtracting the average RTs when no TMS was delivered ($RT_{SOA,\ Site} - \text{mean } RT_{No\ TMS}$). Positive values therefore indicated that TMS caused a relative slowing of RTs, and negative values indicated a speeding of RTs. Conditions in which normalized RTs were substantially greater than zero, as revealed through a one-sample *t* test, indicated that the TMS pulse had a detrimental effect on the neural processing necessary for the given task. However, TMS pulse delivery can itself be startling, since it is accompanied by a loud click, nerve stimulation of the scalp, and possible muscle contraction. It remains possible that any observed effects of TMS, relative to the no-TMS conditions, could be due to these confounding factors. In order to control for this possibility, we had each subject perform the control task twice: once while area MT/MST was stimulated and once while the vertex was stimulated. Any differences between these two conditions observed in a single subject would suggest that MT/MST stimulation has an effect on neural processing beyond the superficial effects of TMS delivery. For this reason, TMS site was treated as a within-subjects variable. In order to maximize error degrees of freedom for statistical testing, and because none of our hypotheses involved the time course effects of TMS, we tested SOA as a between-subjects variable.

To confirm that MT/MST stimulation was impairing motion processing more than vertex stimulation was, normalized RTs were analyzed using a 2 × 4 ANOVA with TMS site as a within-subjects variable and TMS SOA as a between-subjects variable. Results revealed a main effect of TMS site. Across all SOAs, RT performance was significantly slower when TMS was applied to MT/MST rather than to vertex [$F(1,24) = 4.273$, $p < .05$; see Figure 3A], indicating that motion judgments were more impaired by MT/MST stimulation than by vertex stimulation. The effect of stimulation did not depend on TMS SOA [$F(3,24) = 0.677$, $p > .5$], and no TMS site × SOA interaction was seen [$F(3,24) = 0.190$ $p > .5$]. Nonetheless, the normalized RTs in the 0- and 50-msec MT/MST conditions appeared to be substantially greater than zero, indicating that these responses were slower than those in the no-TMS condition. Post hoc one-sample *t* tests confirmed that MT/MST stimulation produced responses that were significantly slower than no-TMS responses in the 0-msec SOA [$t(82) = 2.698$, $p < .01$] and 50-msec SOA [$t(83) = 2.757$, $p < .01$] conditions.

To further demonstrate that TMS had a detrimental effect on motion processing, and to rule out the possibility that the relatively faster responses observed in the vertex stimulation condition were due to speed/accuracy trade-offs, the same analysis was performed using accuracy scores as a dependent measure. Whereas there was no significant difference in accuracy across TMS sites [$F(1,24) = 1.624$, $p > .2$] or main effect of TMS SOA [$F(3,24) = 0.553$, $p > .5$], there was a significant TMS site × SOA interaction [$F(3,24) = 3.103$, $p < .05$]. TMS appeared to cause a drop in accuracy at 0-msec SOA when MT/MST was stimulated, whereas no drop in accuracy at 0-msec SOA was observed when vertex was stimulated (Figure 3B). A post hoc independent-samples *t* test confirmed this interpretation [$t(165) = 2.117$, $p < .05$].

The analysis of normalized RTs revealed that, regardless of SOA, subjects were slower to make motion judgments when MT/MST was stimulated than when vertex was stimulated. In addition, subjects were never more accurate in their motion judgments when MT/MST was stimulated than when vertex was, ruling out the possibility that any observed effects on RTs were due to speed/accuracy trade-offs. These results confirm that MT/MST had been sufficiently localized and that the TMS pulse strength was sufficient to disrupt the motion processing that occurs within MT/MST.

Implied Motion and Object Categorization Tasks

In order to assess whether judgments of implied motion were impaired by disruption to MT/MST, it was necessary to compare performance on an implied motion discrimination task with performance on a control task using qualitatively similar visual stimuli. For this purpose, we employed a control task in which subjects made judgments for which the direction of implied motion was irrelevant—for example, simply judging whether the subject in each image was a person or an animal. Raw RT and accuracy measurements for the implied motion and object categorization tasks are displayed in Table 1.

RTs were again normalized by subtracting the mean RT in the no-TMS and task conditions from each RT in the remaining TMS SOA, site, and task conditions for each subject ($RT_{SOA, Site, Task}$ − mean $RT_{No TMS, Task}$). As before, it was necessary to control for the startling effects of TMS pulse delivery by contrasting MT/MST with vertex stimulation for each subject. As such, TMS site was treated as a within-subjects variable. Similarly, it was important to statistically control for any potential difference in the level of difficulty of one task from that of the other. This was accomplished by contrasting the performance of the implied motion task with that of the object categorization task for each subject. Thus, a significant task × TMS site interaction would reveal that the difference in within-subjects task performance varies with TMS site and would be evidence that TMS stimulation of area MT/MST affects implied motion judgments and object categorization judgments differently. The presence of either a person or an animal was the only relevant difference between the two tasks that the subjects were asked to judge. As before, SOA was treated as a between-subjects variable.

Normalized RTs were analyzed using a 2 × 2 × 4 ANOVA, with task and TMS site treated as within-subjects variables and TMS SOA as a between-subjects variable. A significant task × TMS site interaction was seen [$F(1,24) = 4.994$, $p < .05$; see Figure 4]. In addition, there was a main effect of TMS location [$F(1,24) = 5.817$, $p < .05$], as well as of task [$F(1,24) = 5.416$, $p < .05$]. In the no-TMS condition, subjects responded more slowly in the implied motion task than in the object categorization task (M = 55 and 17 msec, respectively). No effect of TMS SOA was observed [$F(3,24) = 0.100$, $p > .9$]. When the same analysis was performed using raw accuracy scores as a dependent measure, no significant results

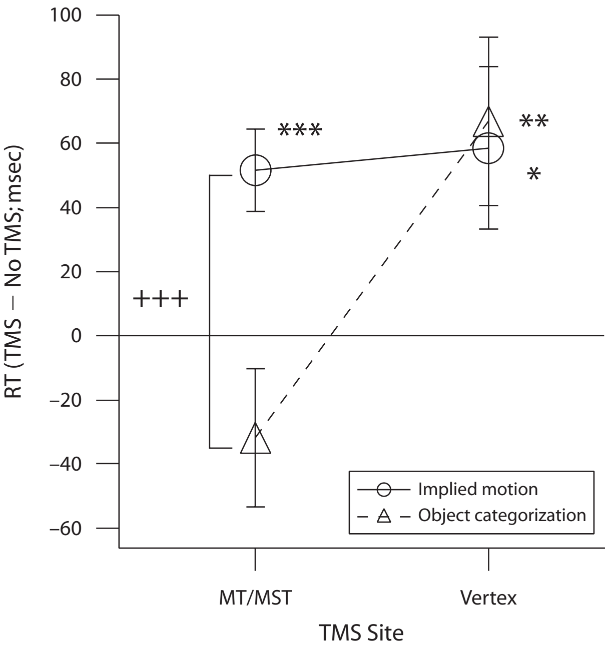

Figure 4. Results from the implied motion discrimination and object categorization tasks show a significant transcranial magnetic stimulation (TMS) site × task interaction, main effect of task, and main effect of TMS site. Mean RT differences from the no-TMS condition are displayed by TMS site and task. Relative to vertex stimulation, MT/MST stimulation had no appreciable effect on the RT at which judgments of implied motion were reached. However, relative to vertex stimulation, MT/MST stimulation appeared to enhance performance in the object categorization task. Error bars indicate ±1 standard error of the mean and contain both within-subjects and between-subjects variance. Significance is indicated by (*; +++) $p < .001$, (**) $p < .01$, (*) $p < .05$. (*s indicate one-sample *t* tests; +s indicate independent-samples *t* tests.)**

were found, suggesting that the significant differences in RTs were not due to speed/accuracy trade-offs.

When TMS was delivered over MT/MST, there was no effect on subjects' abilities to perform the implied motion discrimination task, in comparison with TMS delivery to vertex stimulation. In both cases, however, post hoc one-sample *t* tests revealed that performance in the implied motion task was slower relative to no-TMS, regardless of whether MT/MST [$t(479) = 3.613$, $p < .001$] or vertex [$t(415) = 2.492$, $p < .05$] was stimulated, suggesting that this impairment was due to the superficial effects of TMS pulse delivery itself, and not necessarily to the disruption of underlying neural activity. During the object categorization task, subjects responded slightly more quickly when TMS was delivered over MT/MST than in the no-TMS condition. However, using data from when vertex was stimulated in the object categorization task, we conducted a post hoc one-sample *t* test that revealed that, in comparison with RTs in the no-TMS condition, TMS caused a significant slowing of RTs [$t(410) = 3.269$, $p < .01$] that was comparable to performance in the implied motion task. With data from when TMS was delivered over MT/MST, a post hoc independent-samples *t* test confirmed that subjects were significantly faster at performing object categorization judgments than implied motion judgments [$t(898) = 4.038$, $p < .001$].

DISCUSSION

Previous fMRI studies have shown that MT/MST exhibits greater activity when subjects view static images that imply motion than when they view images that do not (Kourtzi & Kanwisher, 2000; Senior et al., 2000). TMS over MT/MST has been shown to disrupt performance in tasks relating to the perception of motion (Beckers & Hömberg, 1992; Beckers & Zeki, 1995; Campana et al., 2002; Hotson & Anand, 1999; Hotson et al., 1994; Théoret et al., 2002); we therefore hypothesized that TMS over MT/MST would influence performance in an implied motion discrimination task. To verify subjects' behavioral reports that their perceptions of actual motion were disrupted by the TMS pulse, we also asked subjects to perform a motion discrimination task. In this control task, MT/MST stimulation caused a significant slowing in RTs and a drop in accuracy relative to vertex stimulation, indicating that MT/MST had indeed been correctly targeted and successfully disrupted in this experiment. However, there was no substantial difference in the ability of subjects to perform the implied motion discrimination task when the effects of MT/MST stimulation were compared with those of vertex stimulation. This lack of a TMS effect in the implied motion discrimination task suggests that MT/MST is not involved in the early cognitive stages (<150 msec) of processing static images that imply motion. However, it is possible that MT/MST is required for discriminations of this type at later time points during processing (Lorteije et al., 2006). These results suggest that the activation of MT/MST when static images are viewed (Kourtzi & Kanwisher, 2000; Senior et al., 2000) may be due to top-down effects, such as motion priming, visual attention to motion features, or the imagination of motion.

This result is in apparent conflict with a similar study, in which rTMS was shown to disrupt the misremembering that occurs during a representational momentum task, during which subjects judged whether two images separated by 250 msec were the same or different (Senior, Ward, & David, 2002). If motion in an object is implied—through either a static image that strongly suggests motion or a series of static images that elicits the perception of an apparent motion—subjects tend to misremember the final location of the object as having been farther along its predicted trajectory (Freyd, 1983; Freyd & Finke, 1984; Freyd & Pantzer, 1995; Freyd et al., 1988). More specifically, in cases in which the object in a second image (probe) is displayed as being farther along the trajectory of motion implied in the first image, subjects typically have a difficult time correctly discriminating one image from the other. However, when subjects receive rTMS over MT/MST before the probe image is displayed in a representational momentum task, subjects are able to more quickly identify forward probes as being different (Senior et al., 2002). Although the present task and the method used in Senior et al. both address the extent to which MT/MST is involved in the processing of static images suggestive of movement, the present study relies on a judgment about the picture itself, rather than a comparison with an image stored in short-term visual memory. In this sense, TMS in a representational momentum task would disrupt the processing of apparent motion rather than that of implied motion. If TMS over MT/MST were to disrupt either the storage process or the comparison process, then it is plausible that TMS could impair performance in a representational momentum task without affecting performance in an implied motion discrimination task.

The results of the present study demonstrate that the disruption of MT/MST processing fails to affect the speed or accuracy at which subjects can make implied motion judgments. However, in an fMRI study conducted by Kable, Lease-Spellmeyer, and Chatterjee (2002), subjects performed a conceptual matching task with either action pictures or object pictures. Greater activation in MT/MST was found for conceptual matching involving action pictures than for conceptual matching involving object pictures. In light of the present study, the greater activation seen in Kable et al. (2002) would likely be due to subjects, having been exposed to pictures that imply motion, triggering the various extraneous top-down effects that Kourtzi and Kanwisher (2000) propose, and not specifically due to the underlying conceptual task.

Although TMS stimulation over MT/MST appeared to have no effect on subjects' ability to discriminate implied motion, it did improve their ability to classify images as containing either an animal or a person. It is highly unlikely that this result can be attributed to differences in task difficulty between implied motion judgments and object categorization judgments. The same tasks were performed while a neutral site was stimulated (i.e., the vertex), and there was virtually no difference in task performance. Furthermore, the improved ability to make object classification judgments corresponds nicely with and generalizes the results observed in Walsh et al. (1998), in which TMS stimulation over MT/MST actually enhanced color–form conjunction searches. Although the present study failed to show that resources from MT/MST are employed to perform an implied motion discrimination task, it appears that disabling MT/MST facilitates activation of the ventral stream pathways necessary for assessing object identity. It is unclear, however, whether this result depends on the presence of implied motion. An interesting question for future research is whether disabling ventral stream pathways might improve the efficiency with which motion or implied motion judgments are made. Specifically, PET and fMRI studies have implicated the inferior temporal cortex in the region of the fusiform gyrus (Brodmann's Area [BA] 37) as being associated with object identification (Büchel, Price, & Friston, 1998; Moscovitch, Kapur, Köhler, & Houle, 1995). The ability to name objects—but not to read words or identify colors—is disrupted when TMS is applied over a ventral processing area (BA 37), demonstrating that this region is functionally involved in the cognitive processing of object identification (Stewart, Meyer, Frith, & Rothwell, 2001). In the same manner that MT/MST disruption improved object categorization performance in the present experiment, it may be the case that TMS stimulation over BA 37 actually improves performance in motion discrimination tasks.

Finally, studies in which TMS to MT/MST are applied while subjects make judgments about visual stimuli that are moving—such as motion discrimination of random-dot cinematograms presented at low levels of motion coherence (Hotson & Anand, 1999; Hotson et al., 1994)—show disruption at an SOA as early as 100 msec. In contrast, when random dot motion is presented at 100% coherence, TMS over MT/MST disrupts motion processing at 0-msec SOAs, but fails to disrupt motion processing at later SOAs (Beckers & Hömberg, 1992; Beckers & Zeki, 1995). The results of the motion discrimination task in the present study shed light on the discrepancy between the work of Hotson (Hotson & Anand, 1999; Hotson et al., 1994) and Beckers (Beckers & Hömberg, 1992; Beckers & Zeki, 1995). In the present study, an in those performed by Beckers, 100% coherent motion was used, and motion disruption occurred at 0-msec SOA. It is possible that stimuli that have less than 100% coherence, like those used by Hotson, require reentrant processing into V1 before motion judgments can be made, thereby delaying the onset of the temporal window during which MT/MST disruption may affect these judgments. Therefore, the time course of TMS effects over MT/MST could depend on the amount of coherence and visual noise present in the stimulus display.

In summary, we observed that TMS stimulation over MT/MST disrupted motion processing and facilitated ventral stream processing, but failed to affect performance in an implied motion discrimination task. These findings suggest that MT/MST is not directly involved in the visual processing of implied motion at early time points (<150-msec SOA). Rather, it appears that the previously reported increase in MT/MST activation associated with implied motion may be due to top-down effects (Kourtzi & Kanwisher, 2000) that are irrelevant to the judgment of implied motion. In addition, these results provide further support for the finding that disruption of MT/MST facilitates ventral stream processing (Walsh et al., 1998).

AUTHOR NOTE

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