RESEARCH ARTICLE

Nestor Matthews · Bruce Luber · Ning Qian
Sarah H. Lisanby

Transcranial magnetic stimulation differentially affects speed and direction judgments

Abstract This study was conducted to determine whether humans' judgments about the speed and direction of moving stimuli was differentially affected by transcranial magnetic stimulation (TMS). Subjects viewed two successively presented moving stimuli that differed from each other both in speed and direction of motion. Single-pulse TMS was applied either medially (approximately 2 cm above the inion) or laterally (approximately 5 cm lateral to and 4 cm above the inion), while subjects judged the speed and direction differences. The physical stimulation (visual and TMS) was identical on the two tasks, as was discriminability (d') when TMS was not applied. We found significant criterion (β) shifts on the speed discrimination task at both stimulation sites. Specifically, on TMS trials the proportion of "slower" judgments increased significantly, consistent with subjective reports that stimuli often appeared to slow when TMS was applied. The subjective reports indicated no corresponding change in perceived direction. We also found that speed discriminability was impaired significantly more than direction discriminability, but only when TMS was applied medially. Indeed, after controlling for TMS-related changes in reaction time, speed discriminability was impaired significantly, while direction discriminability remained largely intact. This dissociation suggests that the sensory response constraining speed discrimination is at least partially independent from the sensory response constraining direction discrimination. Combined with previous psychophysical data, the present data suggest a double dissociation between speed and direction discrimination in humans.

Keywords Transcranial magnetic stimulation · Motion · Perceived speed · Perceived direction · Speed discrimination · Direction discrimination · Human

N. Matthews (✉) · N. Qian
Center For Neurobiology and Behavior,
Columbia University, USA
e-mail: matthewsn@denison.edu
Tel.: +1-740-5875782, Fax: +1-740-5875675

B. Luber · S.H. Lisanby
Department of Psychiatry, Columbia University, USA

B. Luber · S.H. Lisanby
Department of Biological Psychiatry,
NY State Psychiatric Institute, USA

N. Qian
Department of Physiology and Cellular Biophysics,
Columbia University, USA

N. Matthews
Department of Psychology, Denison University, Granville,
OH 43023, USA

Introduction

It is well known that certain cells in the primate visual pathway respond maximally to particular *combinations* of speed and direction (Maunsell and Van Essen 1983; Mikami et al. 1986; Rodman and Albright 1987; Perrone and Thiele 2000). Neural computational work has suggested that a population of such cells could reliably estimate stimulus velocity, i.e., the vector incorporating speed *and* direction of motion (Heeger 1987). To the extent that judgments about velocity (i.e., speed and direction) depend on a population response in which the speed and direction of motion are combined, one might expect speed discrimination and direction discrimination to covary. Indeed, previous studies have shown that lesions to area MT in the macaque monkey generate impairments on speed (Merigan et al. 1991; Orban et al. 1995) and direction discrimination (Newsome and Pare 1988; Lauwers et al. 2000). Morevoer, covariations between speed and direction discrimination (De Bruyn and Orban 1988; Festa and Welch 1997), and other similarities between these two tasks (Watamaniuk and Duchon 1992; Smith et al. 1994; Festa and Welch 1998), are well documented in the human psychophysical literature.

A recent psychophysical study, however, has suggested that speed discrimination and direction discrimination do not always covary (Matthews and Qian 1999). Specifically, that study indicated that direction differences were significantly more discriminable when the stimuli moved

cardinally (i.e., vertically or horizontally) than when the stimuli moved obliquely (i.e., diagonally), while speed differences were equally discriminable in the cardinal and oblique conditions. The finding that the "oblique effect" in direction discrimination (Ball and Sekuler 1987; Matthews and Welch 1997) is not paralleled in speed discrimination argues against the notion that the two tasks are constrained by a completely shared sensory response. Although the neural substrate of that (Matthews and Qian 1999) psychophysical dissociation is not presently known, there is some physiological evidence for at least a partial segregation of speed and direction tuning in the primate cortex. For example, Lagae, Raiguel, and Orban (1993) identified certain MT cells that retain their direction selectivity over a broad (i.e., 100-fold) range of speeds. Conversely, Cheng, Hasegawa, Saleem, and Tanaka (1994) found that V4 cells, which are not well tuned for direction, are speed tuned. It is possible that such cells (Lagae et al. 1993; Cheng et al. 1994), which respond to just one of the two motion attributes (i.e., speed or direction), could generate different constraints for speed and direction discrimination.

In the present study, the sensory responses that constrain speed and direction discrimination were probed with single-pulse transcranial magnetic stimulation (TMS). TMS may be thought of as a technique for transiently adding "noise" to neural processes (Kammer and Nusseck 1998), and it has long been known that TMS can induce measurable visual disturbances (Amassian et al. 1989). Although some earlier studies (Beckers and Homberg 1992; Hotson et al. 1994; Beckers and Zecki 1995; Hotson and Anand 1999) had focused on whether TMS can perturb the identification of gross direction differences (i.e., 90° or more), none had attempted to create perturbations in the angular resolution of the motion system (i.e., the ability to see direction differences of only a few degrees). Moreover, none of the previous studies had directly assessed whether the sensory response to direction and speed might be differentially affected by TMS. Here we report that, while TMS had no affect on perceived direction, TMS reliably induced a slowing of perceived speed. The subjects' reports of this TMS-induced change in perceived speed were corroborated by significant criterion-shifts (i.e., an increase in the proportion of "slower" responses) on the speed-discrimination task. Also, after controlling for TMS-related changes in reaction time, we found that TMS significantly impaired discriminability (d') on the speed-discrimination task, but not on the direction-discrimination task. This dissociation is inconsistent with the hypothesis that the same sensory response constrains performance on speed and direction discrimination tasks. Furthermore, combined with the earlier psychophysical data (Matthews and Qian 1999), the present data complete a double dissociation between the two tasks: Speed discrimination can be affected while direction discrimination remains intact, and vice versa.

Materials and methods

Subjects

N. Matthews, B. Luber, and three na subjects were participants. Each subject underwent a physical and neurological examination and was medically screened for history of neurological disorder (including seizures), DSM IV axis I psychiatric disorder (SCID-NP), serious medical illness, and use of prescription medications in the preceding 4 weeks. All had normal or corrected-to-normal vision. The subjects' mean age was 38.5 years (SD, ±10.3 years). Four of the five subjects were male. All subjects gave their informed consent before participating in the study. The study was approved by the Internal Review Board of the New York State Psychiatric Institute and was therefore performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Visual stimulation and tasks

The experiment was conducted on a 21-inch (53.34 cm) Viewsonic P817 monitor that was controlled by a Macintosh G4 computer and software from the psychophysics toolbox (Brainard 1997; Pelli 1997). The vertical refresh rate of the monitor was 120 Hz, and the spatial resolution was 1024×768 pixels. In a well-lit room, subjects viewed the monitor through a circular tube with an inner diameter of 10 cm. A chin rest helped to stabilize head position at 57 cm from the monitor.

The stimuli were random-dot cinematograms (RDCs) that produced a compelling sense of translational motion. Each RDC consisted of dots that appeared darker than the light-gray surround (33 cd/m²). All dots within an RDC were presented at a single luminance, which randomly varied between 0.83 and 10.5 cd/m² across RDCs, thereby creating Michelson contrasts between 95% and 52%, respectively. Each dot was a 2×2-pixel square (approximately 5 arc min on each side). There were 25 dots (±30%, randomly) per RDC, making the mean dot-density approximately 3.5 dots/deg², as the dots were presented within a circular virtual aperture having a diameter of 3°. Dots moving out of the aperture "wrapped around" to the opposite side. Subjects foveally viewed the motion stimuli, and a circular fixation dot (11.5 cd/m², 48% contrast) in the center of the aperture helped to stabilize eye position.

Subjects pressed a button to begin each trial. A trial comprised two successively presented RDCs. Each RDC was shown for 200 ms (24 frames), and the interstimulus interval varied from 500 to 700 ms, randomly. On every trial, two new and unique RDCs were generated. The two differed from each other in both speed *and* direction, with the speed and direction differences being completely decorrelated from each other. Since the RDCs that were presented on the speed and direction discrimination tasks were generated from the same algorithm, there were no statistical differences between the RDCs on the two tasks. Consequently, the speed and direction discrimination tasks differed solely in the instructions to the subjects. On the speed-discrimination task, subjects indicated whether the second stimulus was faster or slower than the first by pressing, respectively, the "2" or the "0" key on a number pad. On the direction-discrimination task, subjects indicated whether the direction of the second stimulus was clockwise or anticlockwise to the first by pressing, respectively, the "2" or the "0" key on a number pad. All responses were made with the right hand, and auditory feedback was provided after each response on both tasks. Subjects were told that, although reaction time was being measured, accuracy was of paramount importance.

Since TMS would be applied during the second RDC on each trial, it was critical that the first RDC not contain sufficient information to accurately perform the task. Accordingly, on each trial, one speed was selected randomly from an array of speeds (6°/s, 7°/s, 8°/s, or 9°/s), and the other differed (faster or slower) by the threshold value predetermined for each subject. (The threshold estimation technique is described below, in the Procedures section.)

In this way, even if a subject could discern that the first RDC moved faster (or slower) than the mean speed, there would nevertheless be a 50% chance that the second RDC was slower (or faster). Thus, knowledge about the mean speed and the first speed could not be used as the basis for accurate speed judgments. A conceptually similar approach was adopted for the direction differences. Specifically, on each trial, one direction was randomly selected from the full 360° range, and the other direction differed (clockwise or anticlockwise) by the threshold value predetermined for each subject. This prevented subjects from using the mean direction and the first direction as the basis for direction judgments. In short, to reliably make correct responses on either task, subjects were forced to extract information from the second RDC, when TMS was being applied.

Several nonmotion cues can covary with the speed of motion. One such cue, a "hop-size" cue, arises when the speed difference between two RDCs is achieved solely by varying the distance of the dots' frame-to-frame displacement (i.e., the hop size). We eliminated hop-size cues by using two different spatiotemporal configurations to generate the RDCs on each trial. Specifically, one RDC contained dots that "hopped" on each frame (120 Hz), and the other RDC contained dots that hopped a larger distance only once every two frames (60 Hz). This two-fold difference in the effective frame rate allows speed differences to be decorrelated from hop-size cues, so long as the speed differences are less than two-fold – which was the case in the present study (complete details about these two spatiotemporal configurations are provided by Matthews and Qian, 1999). Another distance-related cue that can covary with speed is the overall traverse: For a given duration (e.g., 200 ms), a greater distance is traversed at faster speeds than at slower speeds. This distance cue can be eliminated by using limited-lifetime dots (i.e., randomly repositioning each dot after a given number of frames) and making the mean dot lifetimes proportionately longer (or briefer) for slower (or faster) speeds. Since human subjects are more sensitive to distance cues than to time cues, it is advantageous to eliminate the distance cue and allow the time cue (i.e., mean dot lifetime) to covary with speed (McKee and Watamaniuk 1994). Accordingly, in one RDC, the lifetime of each dot was randomly selected from a 20-element array of lifetimes that had a mean of five frames. In the other RDC, the lifetime of each dot was randomly selected from a different 20-element array that had a mean proportionately longer (or briefer) than the speed decrement (or increment). The dot lifetimes in each of these arrays ranged from three to seven frames. A control experiment suggested that subjects were unable to accurately use the time-cue (i.e., the difference in mean dot lifetime) as the basis for speed judgments (see Results). Given those results and our controls on the hop size and the traverse, subjects were constrained to base their speed judgments on speed differences rather than on cues that covary with speed.

Transcranial magnetic stimulation

The Macintosh G4 computer that controlled the visual stimuli simultaneously controlled a MagStim 200 stimulator (MagStim Company, Dyfed, UK). On each trial, a single TMS pulse was administered from a 90-mm circular stimulating coil that could generate a peak magnetic field of 2 T. The TMS pulse, which had an estimated rise time of 0.2 ms and a duration of less than 1 ms (Jalinous 1991), always occurred during the second RDC on each trial. Stimulation frequency never exceeded 0.3 Hz. Placed flat and tangential to the scalp, the coil was hand held in the transaxial plane, and the position was further stabilized with a mechanical holder. Coil positions relative to scalp landmarks (international 10–20 system) were noted on a nylon bathing cap that the subjects wore. Subjects also wore earplugs to decrease the sound artifact with coil discharge.

After the subjects were well practiced on the speed and direction discrimination tasks, a 1-h TMS session was conducted for each subject to determine the two positions that would be tested during the main experiment. For one position, which we call the "medial site", the center of the coil was initially placed along the midline, 2 cm above the inion. TMS applied to this site has been shown to cause difficulty in making visual discriminations – an effect that has been attributed to disturbances of V1 (Amassian et al. 1989; Kastner et al. 1998; Kamitani and Shimojo 1999; Corthout et al. 2000). For the other position, which we call the "lateral site", the center of the coil was initially placed 5 cm (left) lateral to and 4 cm above the inion.[1] This scalp location is thought to overlie the human homologue of macaque MT (or V5), as identified in lesion studies (Zihl et al. 1983; Vaina et al. 1990; Regan et al. 1992) and through functional brain imaging (Zeki et al. 1991; Tootell et al. 1995). TMS applied to this area has successfully interfered with motion discrimination (Beckers and Zeki 1995; Hotson and Anand 1999). In the present study, pilot sessions on N. Matthews and B. Luber indicated that, whether TMS was applied to the medial site or to the lateral site, motion stimuli appeared to slow without any change in perceived direction. Each of the three na subjects also spontaneously reported the same perceptual effect. To achieve this perceptual effect, we initially set the field strength of our stimulator to 50% of the maximum, and stair-cased upward in 5% increments until the subject reported that the perception of motion was altered. For each subject, this procedure was repeated at three midline locations in 1-cm rostral steps from the initial medial site, and again over a grid of 12 points (within a radius of 2 cm) around the initial lateral site.[2] For both the medial and lateral sites, the position at which motion was most altered (according to the subject's reports) by the lowest TMS output was used for the rest of the sessions. The optimal intensities typically ranged between 65% and 85% of maximal output. For a given subject, the same intensities were used at the medial and lateral sites. Lastly, we note that several previous TMS studies (Beckers and Homberg 1992; Beckers and Zecki 1995; Walsh et al. 1998) used the terms "V1" and "MT" (or "V5") to refer to what we call the medial and lateral sites, respectively. While V1 is most probably being affected by medial stimulation, portions of Brodmann's area 18 may also receive effective stimulation (Kastneret al. 1998). In addition, although the size of the lateral region where subjects reported difficulty in making motion discriminations was fairly small and well defined, targeting MT is even more problematic than targeting V1. Therefore, in the absence of any anatomical or functional images of our subjects' brains, we prefer to refrain from using names of cortical areas.

Procedures

Before TMS was introduced, each subject completed at least 600 training trials on each task in separate daily sessions. After these training sessions, discrimination thresholds were measured using the method of constant stimuli. For each subject and task, thresholds were based on 240 judgments made across a wide range of stimulus-difference values. In all cases, the responses were significantly ($P<0.05$) fit by a sigmoidal function. Because each fit was significant, we were able to fairly determine each observer's threshold, which was defined as half the stimulus change required to alter the response rate from 0.25 to 0.75. Thresholds so determined corresponded to $d'=0.67$ for each observer and task. Therefore, before TMS was introduced, discriminability (d') was equated on the two tasks for each subject. Typically, the Weber fractions for speed discrimination were between 8% and 12%, while the direction-discrimination thresholds were between 4° and 6°.

In the main experiment, each subject completed five separate daily sessions, with four trial-blocks per session. TMS was applied medially on two of the four trial-blocks, and laterally on the oth-

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[1] Pilot data suggested that unilateral stimulation was sufficient to generate salient changes in the perception of motion. We therefore opted for unilateral stimulation rather than bilateral stimulation in our "lateral" condition.

[2] After locating the optimal position, we measured the area that was effective. We found that 2-cm displacements in any direction from the optimal position (except toward the midline) eliminated the effect.

ers. The order of medial and lateral trial-blocks was randomized across sessions. Trial-blocks began with ten practice trials on each of the two discrimination tasks. During the practice trials, TMS was not applied. Subsequently, TMS was applied at one of six delays relative to the onset of the second RDC (0 ms, 40 ms, 80 ms, 120 ms, 160 ms, or 200 ms) or was not applied at all (i.e., the no-TMS condition). These seven stimulus-onset asynchronies (SOAs) were crossed with four combinations of speed and direction differences (faster/clockwise, slower/clockwise, faster/anticlockwise, and slower/anticlockwise) to produce 28 conditions. Each trial block comprised four sets of these 28 conditions. Subjects judged speed differences on half the sets and direction differences on the others. To eliminate any ambiguity about which task was to be performed, a computer-generated voice announced "please note the task instructions on the screen" at the start of each 28-trial set. The task instructions read either "judge speed" or "judge direction". The instructions were also shown on the screen before and after each trial. Importantly, because the instructions were visible only through the viewing tube, the technician who applied TMS was "blind" to whether the subject was judging speed or direction on each trial.

Data analysis

The data were analyzed with respect to four dependent variables: criterion (β); discriminability (d'); reaction time; and "performance". All four dependent measures were extracted from the same set of observations obtained in the main experiment. The criterion and discriminability values were computed using standard signal-detection procedures (Green and Swets 1966). Hits and false alarms on the speed-discrimination task were operationally defined as "faster" responses made when the second RDC in each trial moved, respectively, faster or slower than the first. On the direction discrimination task, hits and false alarms were operationally defined as "clockwise" responses made when the second RDC in each trial moved, respectively, clockwise or anticlockwise to the first. (It should be noted that hits and false alarms on both tasks were linked to the same motor response – the "2" key on the number pad. Consequently, if subjects used a default motor strategy on TMS trials, such as "press the 2 key after the TMS pulse 2", the change in β would be the same in the two tasks. *Task-specific* changes in β, on the other hand, could not be readily explained by a default motor strategy.) Reaction time was measured so that we could examine whether changes in discriminability could be trivially explained by tradeoffs between speed and accuracy. That is, TMS could add noise that a subject might overcome by taking additional time, thereby producing no change in the hit and false alarm rates upon which our discriminability measure (d') was based. Accordingly, we created a performance index – defined as discriminability divided by reaction time – which controls for speed-accuracy tradeoffs.

On each of the four dependent measures, we first considered the overall effect of TMS on each task. Specifically, for each task and subject, we averaged the data from all conditions on which TMS was applied (i.e., six SOAs and two stimulation sites), then divided by the mean from the no-TMS condition. This division normalizes the TMS data to the no-TMS data. The extent to which the normalized data depart from a value of 1 represents the proportional change attributable to TMS on each dependent measure. By comparing the normalized data from the speed-discrimination task to those from the direction-discrimination task, we sought to determine whether TMS differentially affected the judgments made on the two tasks.

We next investigated whether the place and time of TMS affected the two discrimination tasks. Specifically, after normalizing the data as described above, we conducted separate three-way (Task by Site by SOA: 2×2×6) within-subjects ANOVAs on each of the four dependent variables. For brevity in the Results section, the three-way interactions and the main effect of Site have been omitted, as these were always nonsignificant. Included in the Results are the main effects of Task, SOA (including the analysis of the orthogonal trend components), and the two-way interactions
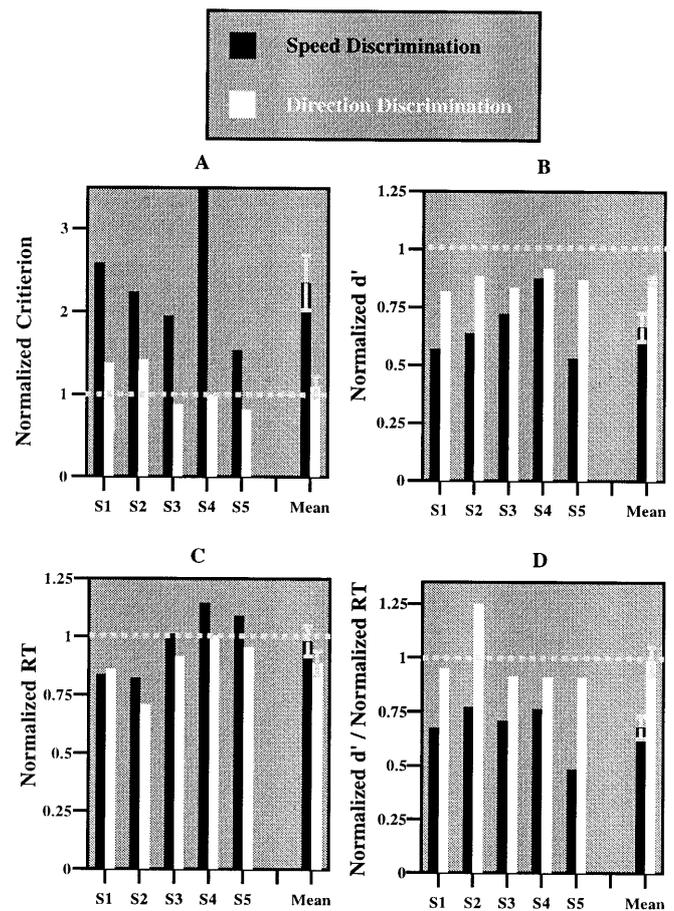

Fig. 1a–d The main effect of TMS on speed and direction judgments. The four dependent variables are shown in separate panels: **a** criterion (β); **b** discriminability (d'); **c** reaction time (*RT*); **d** performance (discriminability/reaction time). Within each panel, normalized data from TMS trials on the speed (*black*) and direction (*white*) discrimination tasks are shown separately for the five subjects (*S1–5*). For each subject and task, the data have been normalized to the no-TMS condition (*dotted horizontal line*) so that the proportional change attributable to TMS can be readily seen. Each datum is based on 960 TMS trials (and 160 no-TMS trials) per subject, per task. The subjects' means (±1 SE) are shown on the *far right side of each panel*. The differential effect of TMS on the two tasks is similar across subjects

that were significant. Two post hoc analyses were also conducted on the discriminability (d') measure and on the performance index. Accordingly, we multiplied the nominal probability of each post hoc test by 2 and evaluated the resultant probability for significance at the 0.05 α-level. In this way, the post hoc tests reported in the Results are corrected for multiple comparisons within each dependent measure.

Results

The overall effects of TMS on speed and direction judgments

The overall effects of TMS on speed and direction judgments can be seen in Fig. 1. In Fig. 1a, the dependent variable is the subjects' criterion (β) – the inclination to

use one of the two response categories on a task. For each subject and each task, the criterion on the TMS trials has been normalized by the corresponding criterion on the no-TMS trials. In this way, the proportional change from the no-TMS condition to the TMS condition can be readily seen for each subject and task. Specifically, the data columns are near or at the dotted line in Fig. 1a when TMS has little or no effect, and depart from the dotted line to the extent that TMS has a large effect. On TMS-trials when the task was speed discrimination, each of the five subjects demonstrated criterion increases (i.e., in Fig. 1a, all black columns are markedly above the dotted line). This criterion shift indicates that subjects favored the "slower" response category on TMS trials and is consistent with each subject's self-report that the motion stimuli often appeared to slow when TMS was applied. Importantly, under identical visual and magnetic stimulus conditions, subjects reported no change in perceived direction, and there was no systematic criterion-shift on the direction-discrimination task (i.e., in Fig. 1a, white columns vary about the dotted line). Indeed, across subjects there is no overlap in the criterion data on the two tasks. The differential effect on speed-criterion and direction-criterion is also clearly evident in the far right columns of Fig. 1a, which indicate the subjects' mean criterion (±1 SE) for the two tasks on TMS trials. These data argue against the possibility that subjects simply resorted to a particular motor strategy (e.g., "press the zero key") on TMS trials, since such a strategy would have generated comparable shifts in β on the two tasks. We believe the data in Fig. 1a and the subjects' self-reports suggest that TMS can systematically alter perceived speed, while having no systematic effect on the perceived direction of the same moving stimulus.

We next analyzed the data to determine whether TMS differentially affected discriminability (d') on the two tasks. The data on discriminability were normalized for each subject and task by dividing the d' value from TMS trials by the corresponding d' value from the no-TMS trials. The normalized discriminability data are plotted in Fig. 1b, where the conventions are the same as those in Fig. 1a. Although TMS impaired discriminability on both tasks (all columns in Fig. 1b are below the dotted horizontal line), the proportional reduction was greater on the speed-discrimination task than on the direction-discrimination task (compare white versus black columns) for each of the five subjects.

We considered the possibility that the overall reduction in discriminability, and the differential reduction in discriminability, could be trivially explained by tradeoffs between speed and accuracy. Accordingly, we determined normalized reaction times for each subject and task, relative to the corresponding no-TMS condition (Fig. 1c). We then computed the ratio between normalized d' (Fig. 1b) and normalized reaction time (Fig. 1c). The result, plotted in Fig. 1d, is a performance index that reflects each subject's accuracy per unit time on each task, relative to the no-TMS condition. Visual inspection of Fig. 1d reveals that TMS consistently generated great-
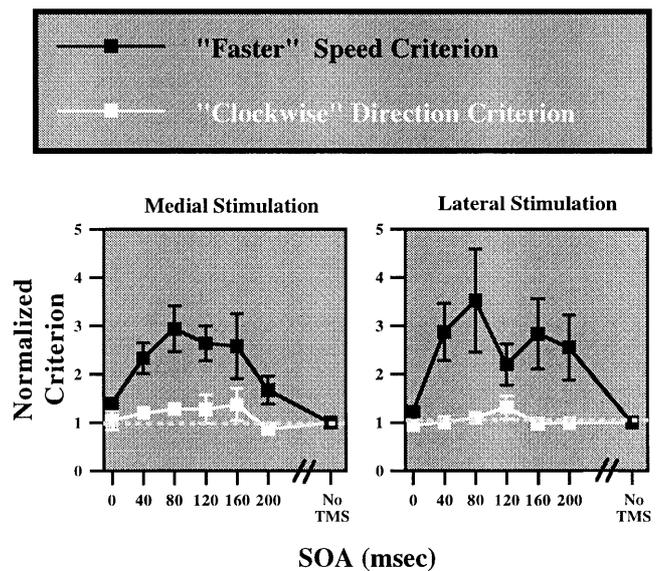

Fig. 2 The effect of stimulation site on criterion. Normalized criterion (β) values are shown separately for the medial (*left panel*) and lateral (*right panel*) TMS conditions at each stimulus-onset asynchrony (*SOA*). The speed (*black*) and direction (*white*) criterion values have been normalized to those from the corresponding no-TMS condition (*dotted horizontal line*, and data on the *far right*). Each datum reflects the mean (±1 SE) of five subjects, and 400 trials (5 subjects × 80 trials per subject). Task-specific criterion shifts are evident at 40 ms and later for both stimulation sites. The increase in the speed criterion coincides with the subjective reports that the motion appeared to slow when TMS was applied

er impairments to performance on the speed task than on the direction task. Indeed, there is no overlap between the speed data (black columns) and direction data (white columns) in Fig. 1d. Moreover, on the direction task, mean performance was comparable on TMS trials and no-TMS trials (in Fig. 1d, the error bar on the far right column overlaps with the dotted horizontal line). These data therefore suggest that, under identical stimulus conditions, TMS can impair speed discrimination without a corresponding impairment in direction discrimination. In the next section, we explore the extent to which this dissociation between speed and direction judgments was a function of the place and time at which TMS was applied. For brevity, we do not present detailed analyses of discriminability (d') and reaction-time, as these are both reflected in our performance index.

The effects of stimulation site and SOA on motion judgments

To determine the extent to which the criterion (β) shifts seen in Fig. 1a depended on where and when TMS was applied, we analyzed the criterion data by stimulation site across the range of SOAs. The data are in Fig. 2, where the medial and lateral stimulation sites are shown in the left and right panels, respectively. Within each panel, the data are presented by SOA. The patterns are clearly similar for the two stimulation sites. Specifically,
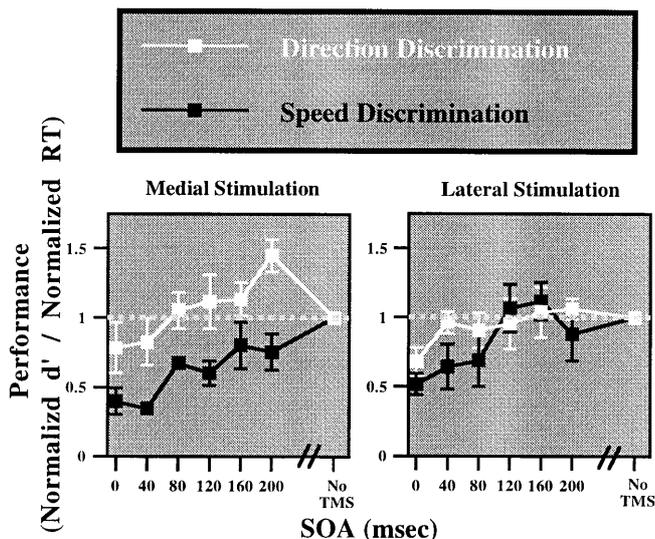
Fig. 3 The effect of stimulation site on performance. Normalized performance (normalized discriminability/normalized reaction time) is shown separately for the medial (*left panel*) and lateral (*right panel*) TMS conditions at each SOA. The speed (*black*) and direction (*white*) performance values have been normalized to those from the corresponding no-TMS condition (*dotted horizontal line*, and data on the *far right*). Each datum reflects the mean (±1 SE) of five subjects, and 400 trials (5 subjects × 80 trials per subject). At any given SOA, TMS suppressed performance on the speed task more than on the direction task, but only when TMS was applied medially. The linear trends in performance were owing to linear trends in discriminability (*d'*), since reaction times were flat across SOAs

the speed criterion (black data points in Fig. 2) increased when TMS was applied at SOAs of 40 ms or later, and the direction criterion remained largely unaffected by TMS (in Fig. 2, white data points are near the dotted horizontal line that represents the no-TMS condition). The ANOVA confirmed what is apparent from visual inspection. Specifically, TMS had a significantly larger effect on the speed criterion than on the direction criterion ($F_{1, 4}$=17.02, P<0.02), and the significant effect of SOA ($F_{5, 20}$=3.50, P<0.02) was owing to a significant quadratic trend component ($F_{1, 4}$=14.95, P<0.02). The ANOVA also confirmed that the task-by-site interaction ($F_{1, 4}$= 0.723, P<0.44, n.s.) was nonsignificant. In short, the data in Fig. 2 indicate that the task-specific criterion shifts were pronounced at SOAs of 40 ms or later and occurred whether TMS was applied medially or laterally.

The task-specific effect of TMS on performance seen in Fig. 1d can also be clearly seen in the left panel of Fig. 3, where the performance data (normalized *d'*/normalized reaction time) are plotted for the medial condition. Visual inspection of the left panel reveals that, at any given SOA, performance on the direction task exceeded that on the speed task, and there is no overlap in the error bars. This task-specific effect, however, was not evident when TMS was applied laterally, as the data and error bars from the two tasks overlap considerably in the right panel of Fig. 3. Although the task-by-site interaction fell shy of significance ($F_{1, 4}$=4.23, P<0.11, n.s.),

post hoc comparisons conducted separately at each stimulation site showed that the effect of task was significant in the medial condition ($F_{1, 4}$=13.29, corrected P<0.04), but not in the lateral condition ($F_{1, 4}$=2.60, corrected P<0.36, n.s.). Therefore, the absence of a significant task-by-site interaction in the omnibus ANOVA is most likely because the task effect was in the same direction at the two stimulation sites, albeit more pronounced medially than laterally. It is similarly probable that the significant omnibus effect of task on performance ($F_{1, 4}$=24.24, P<0.01) was owing to the task-effect in the medial condition.[3]

Lastly, visual inspection of Fig. 3 reveals that, at both stimulation sites and on both tasks, performance tended to increase with SOA. The omnibus ANOVA on performance confirmed that there was a significant main effect of SOA ($F_{5, 20}$=10.23, P<0.001) and that, unlike the quadratic trend in the criterion (Fig. 2), performance was characterized by a significant linear trend ($F_{1, 4}$= 43.08, P<0.003). In principle, this trend could be have been owing either to a linear trend in discriminability (*d'*), or in reaction time, or both. However, ANOVAs indicated that the linear trend component was significant on the discriminability (*d'*) measure ($F_{1, 4}$= 53.49, P<0.002), but not on the reaction-time measure ($F_{1, 4}$=0.01, P<0.98, n.s.), which was flat across SOAs. In the Discussion, we consider the interpretation of the significant linear trends in performance.

Negative SOA experiment

Given that tens of milliseconds are required for a cortical response to visual stimuli, it is surprising that performance in the main experiment was often dramatically impaired at the 0 ms SOA (see Fig. 3). One possible explanation is that TMS induced blinking, and that blinking at 0 ms is most detrimental to performance. We suspect that this is an unlikely explanation, however, since our informal observations indicated that TMS did not typically induce blinking, and because previous work has shown the same deficit for motion (Beckers and Zecki 1995) but not stationary stimuli (Amassian et al. 1989; Masur et al. 1993; Miller et al. 1996). Another possible explanation is that, after a 1-ms TMS pulse is applied, visual neurons may need tens or even hundreds of milliseconds to recover sufficiently to perform subtle speed and direction discriminations. To explore this possibility, we conducted an additional experiment in which TMS was applied either 200 ms *before* the second visual stimulus on each trial (the "–200 ms condition"), or not at all

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[3] The discriminability (*d'*) measure showed a pattern identical to that for the performance index. That is, there was a significant main effect of task on *d'*, and although the task-by-site interaction fell shy of significance, post hoc analyses (corrected for multiple comparisons) indicated that speed discriminability was impaired significantly more than direction discriminability in the medial condition, but not the lateral condition. Normalized mean reaction times were slightly faster on the direction task than on the speed task, and this was equally evident at both stimulation sites.
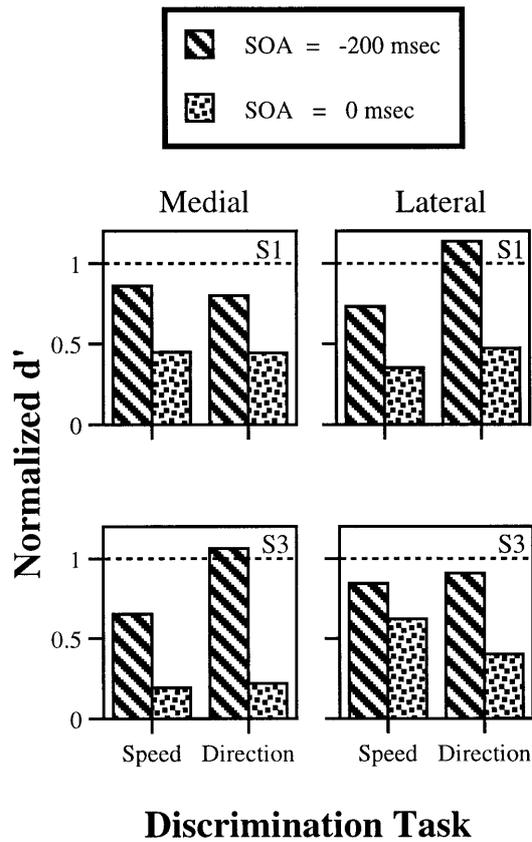
Discrimination Task

Fig. 4 The effect of a negative SOA on discriminability. Data from the negative SOA experiment are shown separately for the medial (*left panels*) and lateral (*right panels*) TMS conditions. Only subjects S1 (*top*) and S3 (*bottom*) participated in the negative-SOA experiment. Discriminability (*d'*) values from the –200 ms condition (*hatched columns*, each based on 112 trials) have been normalized to those from the corresponding no-TMS condition (*dotted horizontal line*). Data from the 0-ms condition in the main experiment have been plotted here (*speckled columns*) for direct comparison. In all cases, discriminability is greater in the –200 ms condition than in the 0-ms condition, demonstraing some recovery from TMS. However, the recovery is not complete after 200 ms, as discriminability in the –200 ms condition is often below that of the no-TMS condition

(the "no-TMS condition"). These two conditions were randomly interleaved within each 112-trial block. Within each trial block, subjects completed two 28-trial sets on speed discrimination and two 28-trial sets on direction-discrimination, randomly, as in the main experiment. Also, the TMS stimulation sites, intensities, and the visual stimuli were the same as in the main experiment. The participants were one of the authors (S1) and one na subject (S3). Each completed four blocks in the medial TMS condition, and four blocks in the lateral TMS condition, randomly.

The data from the negative SOA experiment are plotted in Fig. 4. For each subject and task, discriminability (*d'*) in the –200 ms condition has been normalized to the no-TMS condition, as in all preceding figures. Also, each subject's discriminability (*d'*) data from the corresponding 0-ms condition in the main experiment have

been plotted in Fig. 4 (speckled columns) to facilitate a direct comparison. Visual inspection of Fig. 4 indicates that discriminability was consistently less impaired in the –200 ms condition than in the 0-ms condition (hatched columns are consistently greater than speckled columns). This difference suggests that the sensory responses mediating these subtle motion discriminations had recovered considerably 200 ms after the TMS pulse. However, the data also suggest that complete recovery may require more than 200 ms. This is evidenced by the fact that discriminability in the –200 ms condition is often worse than that in the no-TMS condition (compare hatched columns with horizontal dotted lines in Fig. 4), particularly for speed discrimination.

Control experiments

In principle, it is possible that subjects could have made correct responses on our direction and speed discrimination tasks by using "motion-blind" strategies. In particular, the time-averaged motion of our stimuli contained (nonmotion) orientation cues that covaried perfectly with the direction differences. Similarly, the faster stimulus presented on each trial comprised dots having mean lifetimes briefer than those in the slower stimulus, and this (nonmotion) time cue covaried perfectly with the speed differences, as described above. To determine whether the subjects could make use of these confounding nonmotion cues, we conducted control experiments (without TMS) for the direction (orientation cue) and speed (time cue) discriminations. We discuss each in turn.

In the control experiment for direction discrimination, each of the original five subjects made clockwise/anti-clockwise judgments on 240 trials. On 80% of the trials ("noncatch trials"), the stimuli were the same as in the main experiment. On the remaining 20% of the trials ("catch trials"), the direction of the second stimulus differed from the first by an angle equaling the subject's direction threshold plus 180°. Therefore, since directions differing by 180° share an axis-of-orientation, the orientation cues on catch trials were identical to those on noncatch trials. Consequently, a motion-blind strategy based solely on orientation cues would predict statistically indistinguishable performance on catch trials and noncatch trials. To the contrary, subjects performed significantly ($F_{1, 4}$=289.8, P<0.0001) less accurately on catch trials (mean d'=0.02±0.06) than on noncatch trials (mean d'=0.69±0.03). These data are difficult to reconcile with the possibility that the subjects' direction judgments in the main experiment had been based solely on the motion-blind use of orientation cues.

We adopted a conceptually similar approach in the control experiment for speed discrimination. Each of the original five subjects made faster/slower judgments on 240 trials. On 80% of the trials (noncatch trials), the visual stimuli were the same as in the main experiment. On the remaining 20% of the trials (catch trials), the dots in the second stimulus were stationary, but the dot-lifetimes

were exactly as long as those on corresponding noncatch trials. Therefore, the time cues on catch trials were identical to those on noncatch trials. Consequently, a motion-blind strategy based solely on time cues would predict statistically indistinguishable performance on catch trials and noncatch trials. To the contrary, subjects performed significantly ($F_{1,4}=22.66$, $P<0.01$) less accurately on the catch trials (mean $d'=0.20\pm0.09$) than on the noncatch trials (mean $d'=0.65\pm0.07$). These data are difficult to reconcile with the possibility that the subjects' speed judgments in the main experiment had been based solely on the motion-blind use of time cues.

Discussion

We sought to determine whether humans' judgments about the speed and direction of moving stimuli could be differentially affected by TMS. To permit a fair comparison, stimulation (visual and TMS) on the speed-discrimination task was identical to that on the direction-discrimination task, and we equated discriminability (d') on the two tasks in the absence of TMS. The results indicated that TMS at each stimulation site caused a significant criterion (β) shift in speed discrimination, and this shift was consistent with subjective reports that motion slowed when TMS was applied. The subjective reports indicated no corresponding change in perceived direction, and there was no criterion shift in direction discrimination. Our results also indicated that TMS differentially affected performance (i.e., discriminability/reaction time) on the two tasks. However, unlike the task-specific criterion shift, the task-specific effect on performance depended on *where* TMS was applied. Performance was significantly more impaired on the speed task than on the direction task when TMS was applied medially, but not when TMS was applied laterally. Finally we found that, after averaging across SOAs and stimulation sites, TMS significantly impaired performance on the speed task, while leaving performance on the direction task largely intact. We believe this dissociation suggests that the sensory response constraining speed discrimination is at least partially independent from the sensory response constraining direction discrimination.

Our finding that TMS-generated reductions in perceived speed without altering perceived direction could be due, in part, to our procedure for determining stimulation sites. For example, our data could be attributable to our initial choice of (lateral and medial) coil positions, or our decision to adjust coil positions slightly in accordance with each subject's phenomenal report, or both. We cannot rule out the possibility that TMS at other sites could alter perceived direction, particularly since imaging studies have revealed that many cortical regions are involved in motion processing (Cornette et al. 1998; Orban et al. 1998; Sunaert et al. 1999). However, we note that, although our medial stimulation probably affected both hemispheres while our lateral stimulation probably affected only (or primarily) one hemisphere,

the task-specific criterion shifts were comparable at the two stimulation sites (see Fig. 2). This argues against the possibility that the task-specific criterion shifts were caused by differences between unilateral and bilateral stimulation. We also note that, despite considerable exploration of coil positions, subjects reported no changes in perceived direction at any time in the present study, even when asked explicitly. Regardless of whether future studies reveal TMS-induced changes in perceived direction, we emphasize that the present data alone are sufficient to demonstrate separability in the human visual system's response to speed and direction.

Two SOA-related effects from our main experiment are noteworthy. First, performance on both tasks tended to increase across the range of the SOAs. Second, at the latest SOA (200 ms) there is evidence for a TMS-induced improvement on the direction-discrimination task. We consider each of these SOA-related findings in turn.

As Walsh and Cowey (2000) have noted, a TMS pulse simultaneously activates many neurons over an area of cortex, presumably adding "noise" to the highly coordinated pattern of neural activity required to perform a task. Consequently, the signal-to-noise ratio is lowest when the TMS-induced activation (i.e., the noise) is maximal. As neurons recover over time, the TMS-induced noise declines, and whether TMS continues to have an effect depends on the level of signal required by the task. Therefore, the present finding that TMS induced a greater impairment in speed discrimination than in direction discrimination suggests that a larger signal may be required for speed discrimination. Other clues about underlying neural signals are suggested by the time courses in our TMS data. First, the finding that performance on the speed task was dramatically affected at 0 ms (Fig. 3) while the speed criterion was not (Fig. 2) suggests that different neural signals may underlie speed discrimination and speed perception. This difference is further evidenced by the finding that performance on the speed task tended to increase linearly across the range of SOAs (Fig. 3) while the speed criterion did not (Fig. 2). Similarly, the tendency for performance on the direction task to increase linearly with SOA differs markedly from subjective reports that perceived direction was never altered by TMS. This suggests that different neural signals may underlie direction discrimination and perceived direction. Lastly, the time courses in the TMS data suggest one similarity between speed and direction discrimination. Specifically, although speed discrimination was more impaired than direction discrimination by TMS, performance increased with SOA on both tasks in our main experiment (Fig. 3). One simple explanation is that with increasingly long delays to the TMS pulse, the visual system was able to integrate more frames of the motion sequence, thereby improving the signal-to-noise ratio. Indeed, Festa and Welch (1997) have found that speed and direction discrimination are similarly enhanced by such temporal integration. The finding in our main experiment that performance tended to improve with SOA implies that temporal integration was more

easily achieved before than after the TMS-related noise was applied. Moreover, the data from our negative-SOA experiment (Fig. 4) suggest that TMS-induced impairments in the temporal integration process can be at least residually present for 200 ms or more on these subtle motion-discrimination tasks.

At the latest SOA (200 ms) in our main experiment, performance on the direction task actually improved for each subject when TMS was applied medially. Although TMS-related enhancements have been reported previously for a color-form pop-out task (Walsh et al. 1998), we are unaware of any previously reported enhancements to motion discrimination. Indeed, earlier TMS studies on motion discrimination (Beckers and Homberg 1992; Hotson et al. 1994; Beckers and Zecki 1995; Hotson and Anand 1999) revealed no evidence for TMS-related enhancements. However, there are some important differences between the conditions tested here and those tested in the earlier studies. For example, in one earlier study (Beckers and Zecki 1995), performance in the no-TMS condition was 100% correct, thereby precluding the identification of any TMS-related enhancements. Also, in the other earlier studies on motion discrimination, a single-interval (rather than two-interval) paradigm was used, and subjects were required to make only gross direction judgments, e.g., "up," "down," "left," or "right". To the extent that such gross direction judgments are possible at motion-detection threshold, it is unclear whether TMS in the previous studies had impaired motion detection in general, or direction discrimination, per se. The distinction between motion detection and direction discrimination is nontrivial, since different sensory responses appear to mediate the two tasks (Gros et al. 1998). Given these considerations and the fact that very subtle direction judgments were required only in the present study, it is perhaps unsurprising that the enhanced direction discriminability observed here was not found previously. Although we presently have no explanation for the enhanced direction discriminability at the 200-ms SOA, further exploration of the parameter space may reveal whether the enhancement occurs only when the SOA is temporally proximal to the offset of the visual stimulus.

Several imaging studies have been conducted on speed and direction discrimination in humans. However, these studies have either addressed speed (Corbetta et al. 1990; Orban et al. 1998) or direction (Cornette et al. 1998) discriminations with different subject groups, or have investigated these two discriminations within subjects but under very different stimulus conditions (Huk and Heeger 2000). The present results suggest that future imaging studies may reveal activity differences between speed discrimination and direction discrimination, even under identical stimulus conditions and after equating discriminability on these two tasks within subjects. Indeed, it is not unreasonable to expect that imaging studies will reveal such a dissociation, given that clinical neuropsychological studies have identified other motion-related dissociations. For example, Vaina (1989) has found that occipital-parietal lesions and occipital-temporal lesions, respectively, impair performance on speed discrimination and structure-from-motion tasks. More recently, Vaina and Cowey (1996) have reported that a patient with a unilateral lesion near area MT (V5) performed normally on first-order (luminance modulated) motion stimuli, but was impaired on second-order (i.e., contrast modulated) motion stimuli. Conversely, a patient with an intact area MT (V5) and a unilateral lesion to area V2 performed normally on second-order motion stimuli, but was deficient on tasks involving first-order motion stimuli (Vaina et al. 2000). First-order stimuli were tested in the present study, and the task-specific effect of TMS on performance was significant medially, but not laterally. In the absence of anatomical or functional images of our subjects' brains, however, we refrain from speculating about task-related differences among particular cortical areas.

Finally, our results could have important implications for neural computational models of motion discrimination. In particular, our finding that speed discriminability can be significantly altered by TMS while direction discriminability remains largely intact suggests that models of motion discrimination should posit some independence between the sensory responses constraining each task. Indeed, considerable independence may be warranted, since the TMS-related dissociation reported here is the converse of the dissociation reported earlier: Axis-ofmotion affects direction discrimination, but not speed discrimination (Matthews and Qian 1999). Taken together, the present and previous data suggest a double dissociation between the two tasks: Speed discrimination can be altered without affecting direction discrimination (present study) and vice versa (Matthews and Qian 1999). We believe this double dissociation is nontrivial, given the existence of cortical cells that respond maximally to particular *combinations* of speed and direction (Maunsell and Van Essen 1983; Mikami et al. 1986; Rodman and Albright 1987), and studies showing that MT lesions impair both speed (Merigan et al. 1991; Orban et al. 1995) and direction discrimination (Newsome and Pare 1988; Lauwers et al. 2000).

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