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The Perceived Position of Moving Objects: Transcranial Magnetic Stimulation of Area MT+ Reduces the Flash-Lag Effect

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How does the visual system assign the perceived position of a moving object? This question is surprisingly complex, since sluggish responses of photoreceptors and transmission delays along the visual pathway mean that visual cortex does not have immediate information about a moving object's position. In the flash-lag effect (FLE), a moving object is perceived ahead of an aligned flash. Psychophysical work on this illusion has inspired models for visual localization of moving objects. However, little is known about the underlying neural mechanisms. Here, we investigated the role of neural activity in areas MT+ and V1/V2 in localizing moving objects. Using short trains of repetitive Transcranial Magnetic Stimulation (TMS) or single pulses at different time points, we measured the influence of TMS on the perceived location of a moving object. We found that TMS delivered to MT+ significantly reduced the FLE; single pulse timings revealed a broad temporal tuning with maximum effect for TMS pulses, 200 ms after the flash. Stimulation of V1/V2 did not significantly influence perceived position. Our results demonstrate that area MT+ contributes to the perceptual localization of moving objects and is involved in the integration of position information over a long time window.

Keywords: flash-lag effect, moving objects, MT+, perceived position, TMS

Introduction

The perception of object position involves an accumulation of signals over space and time, in part because of sluggish responses of photoreceptors and noise in neural processing (e.g., Barlow 1958; Burr 1980). For moving objects, this causes additional problems because moving objects change position while signals accumulate. Additionally, delays due to the propagation of signals through several processing stages from the retina to visual cortex mean that the signals arriving at a cortical processing stage at any given time are already "out-of-date."

This problem has been examined extensively using the flash-lag effect (FLE)—a visual illusion in which a moving object is seen ahead of a stationary flash, although the 2 are physically aligned (Fig. 1). The effect has been known since the early twentieth century (Hazelhoff and Wiersma 1924; Metzger 1932; MacKay 1958), but has been the subject of scientific debates more recently in the last 2 decades (reviewed in Krekelberg and Lappe 2001; Nijhawan 2002; Whitney 2002; Nijhawan 2008; Maus et al. 2010). Proposed mechanisms include differential neural processing latencies for moving objects and transient flashes (Purushothaman et al. 1998; Whitney and Murakami 1998; Murakami 2001), averaging of positions over extended time periods (Brenner and Smeets 2000; Krekelberg and Lappe 2000; Brenner et al. 2006), retroactive assignment of integrated positions to earlier time points (Eagleman and Sejnowski 2000), and predictive assignments of perceived positions (Nijhawan 1994, 2008). While the psychophysical literature has remained inconclusive, it seems to be agreed that none of these mechanisms in isolation can explain all of the rich phenomenology, and most likely a mixture of mechanisms is at work in different stimuli used to investigate the illusion. Common to most mechanisms is that the integration of motion signals interacts with the perception of position (Eagleman and Sejnowski 2007). Although psychophysically based models abound, physiological data on the illusion remains surprisingly sparse. In the present study, we used Transcranial Magnetic Stimulation (TMS) to disrupt neural activity in cortical areas MT+ and V1/V2 during a flash-lag task to assess their causal contribution to the integration of motion signals and the perceived position of moving objects.

Area MT+ is strongly selective for visual motion and consists of several retinotopic representations of the visual field with relatively large receptive fields (Huk et al. 2002; Amano et al. 2009; Kolster et al. 2010). Despite the coarse retinotopy, MT+ does represent precise positions of objects in the visual field—especially "perceived" positions (Fischer et al. 2011). TMS studies of MT+ have shown its necessity and temporal specificity for motion perception in motion detection or direction discrimination tasks (Walsh et al. 1998; Sack et al. 2006; Laycock et al. 2007). Also, MT+ is involved in motion-induced mislocalizations of static objects (Senior et al. 2002; McGraw et al. 2004; Whitney et al. 2007), but it is unknown to what extent it plays a role in the integration of motion signals for perceiving positions of moving objects per se. We hypothesized that with repetitive TMS stimulation of MT+ (Experiment 1), the integration of motion signals of a moving object would be impaired and therefore the FLE reduced. Using single TMS pulses (Experiment 2), we measured the temporal specificity of this impairment and examined the temporal tuning of motion integration in the flash-lag phenomenon.

Materials and Methods

Participants

A total of 8 volunteers (3 women) participated in the present experiments. Their ages ranged from 20 to 29 years (mean age = 25.1). Four participants took part in Experiment 1 and 7 in Experiment 2. Three participants took part in both experiments. All participants, except the first author, were naïve as to the purpose and hypotheses of the study and had normal or corrected-to-normal visual acuity. The study was approved by UC Davis and UC Berkeley Institutional Review Boards. Participants were informed about TMS and the experimental procedure;

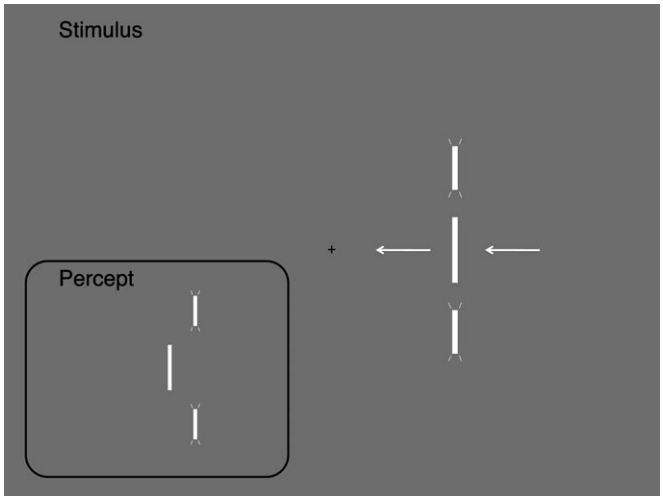

Figure 1. Depiction of the stimulus. A vertical bar moved leftward across the screen toward the fixation point. At a position 5° to the right of the fixation point in Experiment 1 (2° in Experiment 2) 2 flashes appeared above and below the moving bar. The inset shows the percept: When the flashes and the moving bar are physically aligned, the moving bar is perceived to be ahead of the flashes.

they completed a questionnaire to check for potential risks and counter indications.

Stimulus Presentation

Stimuli were presented on a CRT monitor at 100-Hz vertical refresh rate using MATLAB and the Psychophysics toolbox (Brainard 1997; Pelli 1997). Observers sat 80 cm from the screen with their heads rested on a chin and forehead rest.

TMS Stimulation

Biphasic magnetic pulses were delivered using a MagStim Rapid^2 Magnetic Stimulator (The MagStim Company Ltd., Whitland, UK) and a 70-mm air-cooled figure-of-eight stimulation coil. In both experiments, 3 sites were stimulated in separate runs of one session: area MT+ in the left hemisphere, the left occipital pole (area V1/V2), and the vertex. Stimulation sites were localized using the BrainSight frameless stereotactic localization system (Rogue Research Inc., Montreal, Canada). The system tracks the participant's head position and the position of the stimulation coil and presents this information overlaid on an anatomical magnetic resonance imaging (MRI) scan to the experimenter. Standard functional mapping procedures (Huk et al. 2002) were used to identify area MT+ in a functional MRI study prior to the present experiments. The average stimulation site for MT+ was 2.5 cm above and 5 cm left of the inion and for V1/V2 was 3 cm above and 0.5 cm left of the inion. The vertex was identified as the point on the skull, equidistant between nasion and inion and between left and right ear. All participants saw stationary phosphenes with V1/V2 stimulation. The coil position was adjusted, so that phosphenes were perceived on the horizontal meridian in the right visual field and approximately overlapping the position of interest (2°–5° from the fixation point; see below). Of the 8 participants, 4 reported seeing moving phosphenes with stimulation of MT+; no participant saw phosphenes with vertex stimulation.

The TMS coil was held in place by a coil holder with the handle pointing upwards (for MT+ and V1/V2) or backwards (for vertex). TMS pulses were triggered at various timings (see below) by the stimulus presentation software, synchronized to the vertical refresh of the display monitor to avoid artifacts of the magnetic pulses on the CRT monitor. Participants wore earplugs to dampen the clicking noise from the TMS pulse. In Experiment 1, we used a short train of 5 pulses at 10 Hz, that is, 1 pulse every 100 ms at a fixed stimulator output level of 60% of maximum stimulator intensity. In Experiment 2, we used single pulses at 60% of maximum intensity. No participant reported seeing phosphenes at these stimulation levels.

Experiment 1—Is MT+ Involved in the FLE?

Stimuli and Task

In Experiment 1, the stimulus consisted of a vertical white (luminance = 71.3 cdm^{-2}) bar on a mid-gray (10.6 cdm^{-2}) background (0.1° × 1.5° visual angle). Participants fixated a black (0.2 cdm^{-2}) fixation cross in the center of the screen. The bar moved for 500 ms at a constant velocity of 10°/s from the right side of the screen toward the fixation cross (Fig. 1). The trajectory always spanned the distance from 7.5° to 2.5° to the right of the fixation point. About halfway through the motion sequence, at a fixed position 5° from the fixation cross, 2 flashes were presented for 1 refresh cycle of the monitor (10 ms) above and below the moving bar (flashes were vertical bars with dimensions 0.1° × 1°; edge-to-edge separation between bar and flashes = 1°; see Fig. 1). The flashes were always presented in the same position to keep the spatial relation of the trajectory, the flashes, and the retinotopic locus of TMS constant across trials. The timing of the flashes was varied in steps of 20 ms. In 8 different conditions, the flash could be presented up to 100 ms before the moving bar physically reached the flash position, simultaneous and physically aligned with the moving bar, or up to 40 ms after the bar passed the flash position. After each trial, the participants judged by pressing 1 of 2 keys, whether they saw the moving bar to the left or the right of the flashes at the instant the flashes occurred.

Procedure

Each participant performed 7 runs of the psychophysical task. Each run consisted of 160 trials, 20 for each timing of the flash. Runs with TMS over the 3 stimulation sites were alternated with baseline runs without TMS stimulation. The baseline runs between stimulation of different sites were used to allow time between stimulation runs for possible additive and longer lasting TMS effects to wear off, and to check for systematic changes in baseline performance throughout the experiment. The first run was always a baseline run without TMS stimulation. In runs 2 and 4, either MT+ or V1/V2 were stimulated (order counterbalanced across participants), run 6 was vertex stimulation, and the final run was another baseline without TMS. In TMS runs, the first pulse was delivered simultaneous with the onset of the moving bar, the remaining 4 pulses at intervals of 100 ms and the last pulse simultaneous with stimulus offset.

Analysis

The strategy in this experiment was to use a high number of trials in relatively few participants to measure psychometric functions with high precision. Data for each stimulation site from individual participants were fitted with a cumulative Gaussian function. The point of subjective alignment (PSA) is the point where the function crossed 50% left/right responses. Standard errors for PSAs at the group level were estimated by using a bootstrap resampling method. We resampled single trial responses from each participant 10 000 times with replacement and refit the psychometric functions, yielding one PSA for each bootstrap sample. To calculate error bars for the group, single participants' PSAs were sampled from the bootstrapped distributions and averaged. The standard deviation [SD] of the resampled distribution of group means is a bootstrap measure of the standard error of the group mean (Efron 1981). *P* values for pairwise comparisons between stimulation sites and no-TMS conditions were calculated from the proportion of the bootstrap distribution of differences that was greater than zero.

Experiment 2—When Does MT+ Influence the FLE?

In Experiment 2, we aimed to assess the temporal specificity of TMS effects on the FLE. Instead of delivering pulses repetitively throughout the stimulus display, we delivered a single pulse at different time points during a trial.

Stimuli and Task

The stimuli were slightly modified from those in Experiment 1. Again, the moving bar moved linearly toward the fixation cross at 10°/s for 500 ms. After 250 ms, when the bar was in a position 2° from the fixation cross, 2 bars above and below the moving bar were flashed in perfect alignment. The flashed bars were presented for 2 refresh cycles (20 ms) with an edge-to-edge gap of 0.5° to the moving bar. The

moving bar continued to move for another 250 ms, passing the fixation cross before it disappeared from the screen. After another 250 ms, all parts of the stimulus, the moving and the flashed bars were presented motionless and continuously for an adjustment task. The flashed bars were presented in the same position as during the motion sequence, the moving bar was presented in a random position between 1.8° to the left and 0.2° to the right of the flashes. Using a method-of-adjustment task similar to previous studies (Kreegipuu and Allik 2004; Eagleman and Sejnowski 2007; Maus and Nijhawan 2009), participants adjusted the position of this bar using the arrow keys on the keyboard to match their percept of the moving bar in relation to the flashes during the motion sequence. Participants were instructed to foveate the fixation cross throughout both the motion sequence and the adjustment phase.

Procedure

Participants performed 24 trials of the adjustment task without TMS to measure the baseline FLE with this methodology. In the TMS runs, participants were stimulated with one pulse per trial. Stimulus onset asynchronies (SOAs) between the flash and the TMS pulse varied between −200 and +250 ms in steps of 50 ms. Stimulation sites MT+, V1/V2, and vertex were tested in separate runs, with the order of test sites counterbalanced between participants. Each of the 10 pulse timings was repeated 12 times in one run for a total of 120 trials. After the TMS runs, participants performed another 24 trials of the psychophysical task without TMS stimulation (1 of the 7 participants did not perform this test after the TMS runs). Four participants performed 2 sessions of this experiment on separate days.

It is known that auditory stimuli presented in close temporal proximity to the flash during an FLE task bias the perceptual judgments, with flashes being perceived temporally attracted to the auditory stimulus (Vroomen and De Gelder 2004). Since TMS pulses are accompanied by a clicking noise that is audible even through hearing protection, we expected an influence of TMS timing on FLE regardless of the stimulation site. In an additional control experiment, 5 participants who had taken part in Experiment 2 performed 2 runs of the same task, where the single TMS pulse was replaced by an auditory beep (sine wave at 900 Hz, presented over head phones for 15 ms) and presented at the same SOAs.

Analysis

We estimated standard errors for adjustment responses at the group level by using a bootstrap resampling method as for Experiment 1. We resampled data from each participant 10 000 times with replacement, and calculated group means for each resampled set of responses. The SD of the resampled distribution of group means is a bootstrap measure of the standard error of the group mean (Efron 1981). The interaction of pulse timing and stimulation sites was tested with a permutation F-test (Manly 2007); differences between pulse timings and stimulation sites were assessed by non-parametric Friedman and Wilcoxon signed-rank tests; P values for pairwise comparisons between stimulation sites at single pulse timings were calculated from the proportion of the bootstrap distribution of differences that was greater than zero.

Results

Experiment 1

All participants showed a typical FLE, that is, they perceived the leftward-moving bar to be to the left of the flashes, when it was in fact physically aligned. We fitted psychometric functions to each participant's responses to calculate individual PSAs as a measure of the FLE. The magnitude of the FLE did not differ systematically in the baseline runs before, in-between, and after the TMS runs (all $P > 0.1$). We therefore collapsed trials from all runs without TMS and refitted psychometric functions to calculate one score for the no-TMS baseline FLE for each participant. The mean baseline FLE was 42.8 ms (bootstrapped SD = 3.5 ms; see Materials and Methods), indicating that the moving bar was perceived to be aligned, when it was actually, on average, 42.8 ms, or 0.43°, short of the position of the flashes.

Each participant received 5 pulses of 10-Hz TMS stimulation per trial over MT+, V1/V2, and the vertex in separate runs, while performing the localization task. We fitted psychometric functions to individual observers' responses (Fig. 2). Any change in the psychometric function with TMS compared with baseline reflects an influence of TMS on the localization performance. The mean of individual PSAs with stimulation of V1/V2 was 43.5 ms (SD = 2.5 ms), with stimulation of MT+ 34.9 ms (SD = 2.7 ms), and with stimulation of the vertex 49.3 ms (SD = 2.1 ms; see Fig. 3). Stimulation of MT+ reduced the FLE by 21.9% compared with the no-TMS baseline. Pairwise comparisons revealed a significantly reduced FLE with stimulation of MT+ compared with no TMS, $P = 0.031$ and vertex, $P < 0.0001$, but no significant differences between V1/V2 stimulation and no TMS, $P = 0.560$, or vertex and no TMS, $P = 0.939$. MT+ stimulation led to a significantly smaller FLE than V1/V2 stimulation, $P = 0.007$. V1/V2 was marginally different from vertex, $P = 0.048$, but not from the no-TMS baseline conditions (see above).

The slopes of psychometric functions did not differ systematically between different stimulation sites and the baseline

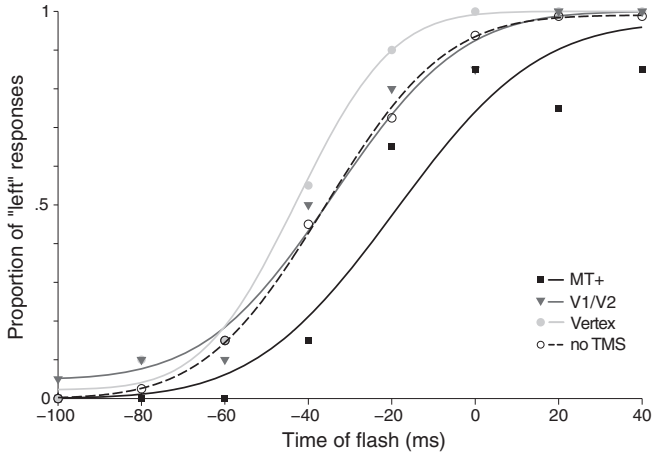

Figure 2. Responses and psychometric functions of one exemplar participant in Experiment 1. The proportion of "left" responses is plotted against the time of the flash relative to the time the moving bar passed the position of the flash. Negative values mean that the leftward-moving bar was still short of the position of the flashes. Responses without TMS are shown in open symbols, dashed line; responses with stimulation of MT+ in black, V1/V2 in dark gray, and vertex in light gray. The bar was perceived as aligned when it was still short of the flash position in all conditions. This mislocalization is reduced with stimulation of area MT+.

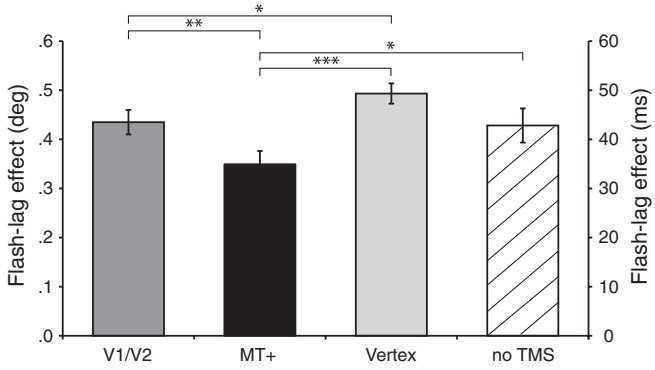

Figure 3. Mean size of the FLE in Experiment 1 with stimulation of V1/V2, MT+, Vertex, and without TMS. Error bars are SDs of the bootstrap distribution (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

runs (all $P > 0.1$), showing that participants' ability to perform the position judgment was not affected by TMS.

Experiment 2

In Experiment 1, stimulation of MT+ reduced the size of the FLE with TMS delivered throughout the stimulus presentation. In Experiment 2, we delivered a single pulse in each trial at a range of pulse timings from 200 ms before to 250 ms after the flash. Single TMS pulses might have more subtle effects, but they offer high temporal precision to allow inferences about the timing of underlying neural processes involved in the FLE.

The mean FLE measured without TMS, using an adjustment method, was 0.38° (bootstrapped SD = 0.01°), or expressed in terms of time, 38 ms. In the test after the TMS runs, the FLE was slightly increased to 0.41° (or 41 ms; SD = 0.02°; see Fig. 4*A*). This difference was not significant, $P = 0.079$ and contrary to what would be predicted from cumulative TMS effects throughout the course of the experiment. The size of the baseline FLE measured with the adjustment task is comparable to the values obtained with the 2AFC method in Experiment 1. Collapsed over all pulse timings, stimulation of MT+ led to the smallest FLE, significantly different from vertex stimulation, two-tailed Wilcoxon signed-rank test $Z = 2.197$, $P = 0.028$. Stimulation of V1/V2 did not differ from stimulation of vertex, $Z = 0.338$, $P = 0.735$.

The mean flash-lag adjustments with stimulation of V1/V2, MT+, and vertex at different pulse timings are shown in Figure 4*A*. A permutation *F*-test revealed no significant interaction of stimulation site and pulse timing, $F = 1.20$, $P = 0.225$. Stimulation at all 3 sites was similarly affected by the different pulse timings; earlier pulses led to smaller perceived FLE. A Friedman test indicated a significant main effect for the timing of TMS pulses on adjustments, $\chi_9^2 = 36.5$, $P < 0.0001$. This is due to the known effects of an auditory sound (like the click produced by the TMS) on the FLE (Vroomen and De Gelder 2004; see Discussion). To confirm this, in a separate psychophysical control session, the FLE was measured with TMS pulses replaced by a beep presented over headphones at the same timings as the TMS. We found the same characteristic slope as in Figure 4*A*, when TMS pulses were replaced by the beep (see Supplementary Data), just as Vroomen and De Gelder (2004) found. Thus, the slope in Figure 4*A* is not due to neural effects of TMS or stimulation of any particular area per se. The critical comparison is therefore between stimulation of MT+ or V1/V2 and vertex stimulation, which was shown not to influence the FLE in Experiment 1.

The net difference in the FLE with visual cortex stimulation relative to vertex stimulation is plotted in Figure 4*B*. The pattern of differences shows a temporal tuning of the TMS-induced reduction in the FLE. We conducted planned pairwise

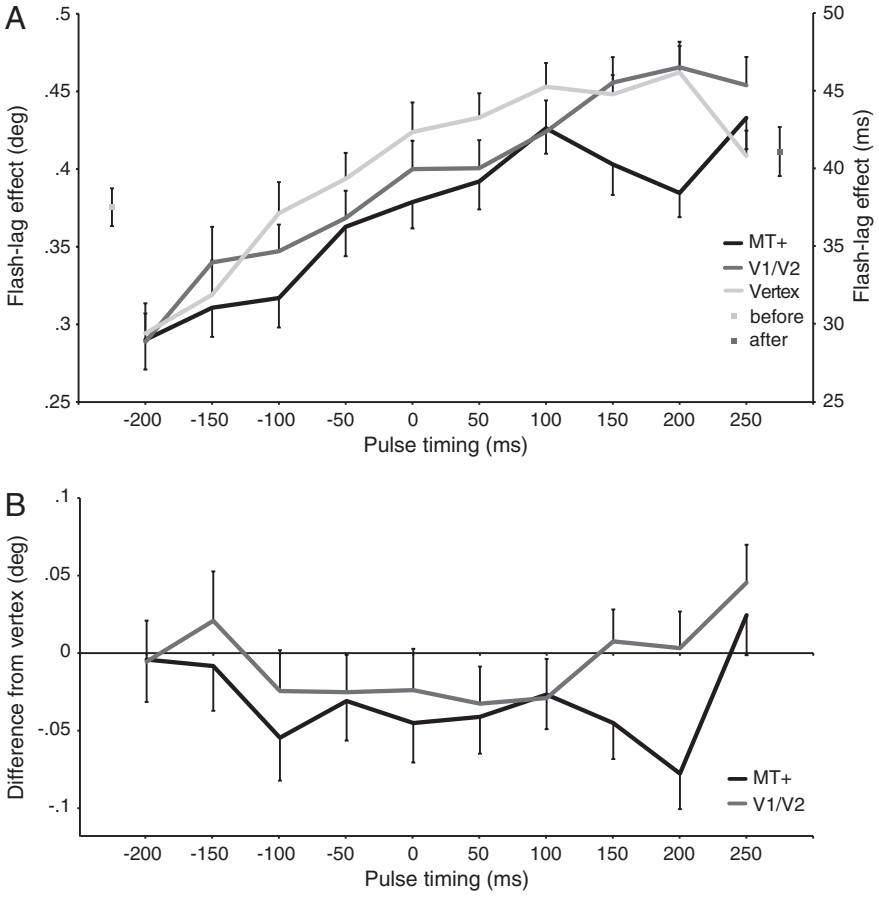

Figure 4. The average flash-lag effect using the method of adjustment in Experiment 2 (*A*). Positive values indicate that participants perceived a FLE—the moving bar appeared to the left of the flashes. Adjustments are shown as a function of pulse timing with stimulation of MT+, V1/V2, and vertex, respectively. The 2 data points to either side show participants' adjustments in trials without TMS, before and after the experiment. Error bars are SDs of the bootstrap distribution (plotted in one direction for legibility). (*B*) The same data as in (*A*), plotted as difference of MT+ and V1/V2 from Vertex.

comparisons of MT+ and V1/V2 stimulation versus vertex stimulation at each pulse timing. MT+ stimulation at 200 ms after the flash caused significantly smaller adjustments, $P = 0.002$, significant after a conservative Bonferroni correction for multiple comparisons (10 pulse timings). The FLE with MT+ stimulation at this time point is reduced by 16.8% relative to stimulation of the vertex. Other pulse timings of MT+ stimulation led to marginally significant effects (uncorrected) at –100 ms ($P = 0.021$), 0 ms ($P = 0.040$), 50 ms ($P = 0.043$), and 150 ms ($P = 0.026$). Stimulation of V1/V2 was not significantly different from Vertex at any pulse timing (all $P > 0.091$, uncorrected), but visual inspection of Figure 4*B* also shows weak temporal tuning of the effect for V1/V2. MT+ stimulation led to significantly smaller FLE than V1/V2 stimulation only with late pulses at 200 ms ($P < 0.001$, Bonferroni corrected) and 150 ms ($P = 0.021$, uncorrected), but not at earlier pulse timings.

Discussion

Summary

The present study provides the first direct physiological evidence for the involvement of area MT+ in the localization of moving objects in the FLE. Experiment 1 showed that repetitive TMS over area MT+ decreased the FLE compared with no TMS or TMS over all other sites. Stimulation of area V1/V2 had only a weak influence on the FLE. However, the lack of significant V1/V2 effects should not be interpreted as hard evidence against an involvement of V1/V2. The speed we used for the moving object (10°/s) is optimal for exciting MT+ neurons, whereas motion-selective neurons in earlier stages prefer slower speeds (Mikami et al. 1986). Furthermore, TMS effects over V1/V2 are highly retinotopically specific; only slight deviations of the stimulated locus from the retinotopic representation of the position of interest might lead to reduced effects of TMS measured here.

In Experiment 2, our goal was to identify the temporal tuning of TMS effects to assess the temporal integration of motion signals for the determination of perceived position. Here, we used an adjustment method; after each stimulus presentation, participants adjusted the position of a bar relative to the position of the flanking flashes to reflect their percept during the TMS trial. Adjustment methods have successfully been used to show small differences in motion-induced mislocalizations by several groups (Kreegipuu and Allik 2004; Shim and Cavanagh 2004; Arnold et al. 2007; Eagleman and Sejnowski 2007; Maus and Nijhawan 2009). Again, we found that TMS over MT+ significantly reduced the FLE. The effect of single pulses was broadly tuned around the time of the flash, with the maximum effect occurring for TMS pulses 200 ms after the flash.

TMS Effects on General Performance

The TMS-induced changes are not due to a general decrement of localization performance or degraded visibility of either the flashes or the moving bar. Either of these would result in shallower slopes of psychometric functions. The slopes of psychometric functions in Experiment 1 did not change with TMS. Consistent with this, a recent study showed that a Vernier task, where the relative position of 2 line segments had to be judged, was not affected by TMS over the occipital pole (Scharnowski et al. 2009).

In Experiment 2, we found a main effect of pulse timing at all stimulation sites on the size of the FLE. Earlier pulses led to smaller adjustment responses. This is due to non-neural effects of TMS, since all sites are equally affected. Each TMS pulse produces an audible click; participants tend to temporally bind the perception of the flash crossmodally to this additional stimulus (Shams et al. 2002). Vroomen and De Gelder (2004) showed that sounds presented shortly before or after the flash gradually attract the flash toward the time of the sound, biasing the FLE to be smaller or larger, respectively. We replicated this finding in a control where auditory beeps were presented instead of TMS pulses. Because auditory stimulation due to TMS was very similar at the 3 stimulation sites, and since vertex stimulation was shown in Experiment 1 to not influence the FLE, we normalized the effects of visual cortex stimulation to vertex stimulation.

TMS Effects on Perceived Contrast and Speed

TMS over V1 (though, not MT+) can result in a decrease of perceived contrast (Harris et al. 2008). Changes in contrast are known to produce changes in perceived speed (Hess 1904). TMS over MT+ (and V3A) can impair speed judgments of a moving stimulus. Stimulation of either area with a short train of repetitive TMS decreases the perceived speed and increases speed discrimination thresholds (McKeefry et al. 2008). The FLE scales with the speed of the moving stimulus (Nijhawan 1994); a decrease of the perceived speed due to TMS is therefore a possible source for the reduced FLE. However, none of the participants in our study reported noticing a disruption of smooth motion or perceptual changes of contrast or speed in the moving stimuli. Assuming that the moving object perceptually still covers the same distance (trajectory length), transient disruptions of smooth motion due to TMS pulses might consist of a brief reduction followed by a brief increase in perceived speed. This pattern would cause decreased, as well as increased FLE magnitudes for different pulse timings. We did not find evidence for this pattern.

Abrupt changes in contrast of the moving object at the same time of the flash can reduce FLE magnitude, although this is due to the role of transient signals on the localization of the moving object, not due to perceptual changes in speed (Maus and Nijhawan 2009). The effect of "physical" speed changes on the FLE has been thoroughly investigated (Whitney et al. 2000). Changes in speed more than 80 ms after the flash do not lead to changes in flash-lag magnitude (cf., Figs 8 and 9 in Whitney et al. 2000). The same holds true for abrupt changes in contrast (unpublished observations). Our peak effect of a reduction in the FLE occurred with TMS pulses 200 ms after the flash. A TMS-induced reduction in perceived speed would therefore occur too late to influence the magnitude of the FLE. While a reduction in perceived speed in this experiment cannot be ruled out, it seems to act in a very different way than a physical change in speed of the moving object. An alternative is that the "perceived position" of the moving object (not its perceived speed) is influenced by TMS pulses over MT+.

Models of the FLE

Two major classes of models have been brought forward to explain the FLE: spatial and temporal models. Spatial models interpret the FLE as a perceptual forward shift of the moving object, possibly to counteract transmission delays of the visual

signal from the eye to cortex. These spatial shifts are thought to occur predictively (Nijhawan 1994, 2008; Chappell and Hine 2004; Kanai et al. 2004; Maus and Nijhawan 2006; 2008; 2009) or retroactively (Eagleman and Sejnowski 2007). In both cases, the forward shift of the moving object is thought to be the result of an interplay of lateral excitation and inhibition in retinotopic maps and/or feedback from higher areas (Kirschfeld and Kammer 1999; Fu et al. 2001; Erlhagen 2003; Kanai et al. 2004; Sundberg et al. 2006; Maus and Nijhawan 2009). Disrupting neural processing in area MT+ might specifically interfere with feedback signals that would usually bias localization on the retinotopic map of primary visual cortex forward in the direction of motion, although the late peak effect at 200 ms in this study does not directly support a predictive account.

The simplest temporal explanation of the FLE is that moving and flashed objects are subject to differential perceptual latencies (Purushothaman et al. 1998; Whitney and Murakami 1998; Whitney et al. 2000; Murakami 2001; Oğmen et al. 2004). If the moving object was simply perceived more quickly than the flash, the flash would be perceived to lag behind. Independently of whether differential latencies are the underlying cause of the FLE, TMS in the present experiment might decrease the size of the effect by selectively delaying the perception of the moving object, thereby leading to a decreased misalignment. Recent studies using TMS have shown that area MT+ does play a role in temporal perception of visual stimuli. Stimulation of MT+ decreased discrimination performance, when observers judged the temporal duration of a visual motion stimulus (Bueti et al. 2008). TMS in that study did, however, not cause a dilation or contraction of the perceived duration of one stimulus over another. To explain our results in terms of changed perceptual latencies, TMS would have to delay the perception of the moving object relative to the flash or speedup the perception of the flash relative to the moving object, both of which seems unlikely.

Other temporal models of FLE are based on temporal integration (Krekelberg and Lappe 1999; Brenner and Smeets 2000; Eagleman and Sejnowski 2000; Krekelberg and Lappe 2000; Whitney et al. 2000; Brenner et al. 2006; Roulston et al. 2006). These models describe the perceived position of the moving object as the outcome of a temporal sampling process that integrates positions over an extended time window. Compared with the flash, which only occupies one position over the course of any integration time window, the moving object is perceived to be ahead. Several variants of temporal integration propose different temporal extents of the integration window, for example, a long window of ~500 ms (Krekelberg and Lappe 2000), a shorter window (Brenner and Smeets 2000), a window that is weighted toward more recently sampled time points (Roulston et al. 2006), or a window that starts only after the flash because the flash somehow "resets" ongoing integration of position (Eagleman and Sejnowski 2000). None of these theories make any explicit predictions about where in the brain the supposed integration of positions occurs.

Even spatial theories of the FLE require some sort of temporal integration, since the amount of the spatial forward shift is based on information from the past trajectory of the moving object, sampled over time. In the present study, we show that TMS over area MT+ reduces the FLE over a long range of time. Furthermore, our result shows that time points, both before and after the flash, are taken into account in the calculation of position. There is a non-negligible reduction of the FLE with pulses as early as 100 ms before the flash, whereas the peak reduction occurs with pulses 200 ms after the flash. This broad temporal tuning is consistent with some theories of temporal integration (Krekelberg and Lappe 1999, 2000). Our finding points to area MT+ as the possible neural site for temporal integration.

Psychophysical results on the FLE are multifaceted and complex; there are good arguments for (and against) most models mentioned above. It is well possible that all models play a role in generating the FLE. Motion-induced spatial shifts in other related phenomena (Ramachandran and Anstis 1990; De Valois RR and De Valois KK 1991; Whitney and Cavanagh 2000; Maus and Nijhawan 2008) cannot be explained by temporal effects. Temporal integration over time is, by definition, necessary to generate motion percepts. The occurrence of the FLE in random motion shows that differential latencies do also play a role (Murakami 2001). Our results demonstrate that the mechanism or likely combination of mechanisms that generate the flash-lag effect are partly implemented in area MT+.

Conclusions

The FLE highlights the important challenges faced by the visual system when attempting to precisely localize the positions of moving objects. Despite an abundance of theories on the FLE inspired by psychophysical experimentation or computational considerations, to date there has been no direct evidence about the involvement of specific brain structures that may cause this illusion in humans. Our results show that the neural mechanisms that the visual system relies on to localize the position of a moving object are implemented in area MT+.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/

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