Neuroscience Letters 490 (2011) 226–230

Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet

# Disruption of MT impairs motion processing

Preston P. Thakral *, Scott D. Slotnick

*Department of Psychology, Boston College, Chestnut Hill, MA, USA*

ARTICLE INFO

*Article history:*
Received 23 July 2010
Received in revised form
20 November 2010
Accepted 25 December 2010

*Keywords:*
Attention
FMRI
MST
Perception
TMS

ABSTRACT

Functional magnetic resonance imaging (fMRI) studies have associated motion processing with cortical region MT+, which includes sub-region MT that preferentially processes motion in the contralateral visual field. Transcranial magnetic stimulation (TMS) has been used to temporarily disrupt MT+ which impaired motion perception, suggesting this region is necessary for motion processing. In the present study, we used fMRI guided TMS to disrupt MT and determine whether this sub-region is necessary for motion processing. On an individual participant basis, MT was localized in each hemisphere using motion related fMRI activity on the posterior bank of the ascending limb of the inferior temporal sulcus. In the first experiment, 1 Hz TMS of left MT preferentially impaired motion detection in the contralateral versus ipsilateral visual field. In the second experiment, single-pulse TMS of MT impaired motion processing to a greater degree than color processing. These results provide convergent evidence that sub-region MT is necessary for motion processing.



Human motion processing region MT+, which has been localized to the ascending limb of the inferior temporal sulcus [34], is comprised of sub-region MT, which processes motion in the contralateral visual field (i.e., left hemisphere MT processes motion in the right visual field and vice versa), and sub-region MST, which processes motion in both the contralateral and ipsilateral visual fields [1,6,10,12,15,20,27]. There is also functional magnetic resonance imaging (fMRI) evidence that attention to motion can increase the magnitude of activity in MT+ [30], and contralateral motion attention effects, presumably reflecting modulation of sub-region MT, have also been reported [26]. It should be noted that sub-region MT can process motion in the ipsilateral visual field to some degree [21,32]; however, this sub-region predominantly processes motion in the contralateral visual field [1,6,10,12,15,20,27].

The preceding fMRI evidence [1,6,10,12,15,20,26,27,30] suggests region MT+, which includes sub-regions MT and MST, is associated with motion processing. However, fMRI is correlational in nature; thus, fMRI activity associated with a given cognitive process may be epiphenomenal [16,19]. If a region is necessary for a given cognitive process, its disruption should impair the corresponding behavioral performance. This type of evidence has been reported in previous studies that have used transcranial magnetic stimulation (TMS) to temporarily disrupt MT+ which impaired motion processing. However, the MT+ target locations in these studies have typically been based on fixed distances from non-brain landmarks such as the inion [7,8,14,33] or subjective measures such as the site of TMS induced motion phosphenes [2,3,11,13,17,23,29], but see [31]. While such techniques might have localized MT+, they may have also stimulated other adjacent neural regions such as motion sensitive extrastriate region V3A. In four recent fMRI guided TMS studies, motion related fMRI activity within the ascending limb of the inferior temporal sulcus [34] was used to specifically target MT+ which impaired motion processing [9,18,22,28]; see also [4]. The latter results provide compelling evidence that region MT+ is necessary for motion processing.

The aim of the present study was to use fMRI guided TMS to selectively target sub-region MT, located on the posterior bank of the ascending limb of the inferior temporal sulcus [5,10,15], to determine whether temporary disruption of this sub-region would be sufficient to produce an impairment in motion processing. As MT is known to predominantly process motion in the contralateral visual field [1,6,10,12,15,20,27], selective disruption of this region should be evidenced by preferentially impaired motion detection in the visual field contralateral to the hemisphere of TMS application. Of relevance, Hotson and Anand [14] reported impaired motion processing in the contralateral visual field following TMS to putative MT+; however, color processing was similarly impaired suggesting a more posterior extrastriate region may have been targeted; see also [7]. In addition, McKeefry et al. [18] used fMRI guided TMS to target MT+ which impaired motion processing in the contralateral visual field, but ipsilateral targets were not presented such that contralateral versus ipsilateral performance could not be evaluated; see also [8,22]. Considering these findings, the present study conducted two experiments to test whether TMS to

* Corresponding author at: Department of Psychology, Boston College, 316 McGuinn Hall, 140 Commonwealth Avenue, Chestnut Hill, MA 02467, USA. Tel.: +1 617 552 9248; fax: +1 617 552 0523.
*E-mail address:* thakralp@bc.edu (P.P. Thakral).

0304-3940/$ – see front matter 
doi:10.1016/j.neulet.2010.12.057

MT would produce a contralateral motion processing impairment (Experiment 1) and to test whether TMS to MT would produce a motion but not color specific impairment (Experiment 2).

*Experiment 1*: Ten participants (8 females, age range 19–28 years) from the Boston College community with normal or corrected-to-normal vision took part in the study (only left MT TMS data were acquired for one participant). The TMS and fMRI protocols were approved by the Boston College and Massachusetts General Hospital Institutional Review Boards, respectively. Informed consent was obtained before each session commenced.

MRI was conducted using a Siemens 3 Tesla Trio Scanner. Functional images were acquired using an echo-planar imaging sequence (TR = 2 s, TE = 30 ms, 64 × 64 acquisition matrix, 30 axial slices, 4 mm isotropic resolution) and anatomic images were acquired using a magnetization prepared rapid acquisition gradient echo sequence (TR = 30 ms, TE = 3.3 ms, 128 sagittal slices, 1.33 mm × 1 mm × 1 mm resolution). fMRI analysis was conducted using BrainVoyager QX (Brain Innovation B.V., Maastricht, The Netherlands). Functional image pre-processing included slice-time correction, motion correction, spatial filtering via convolution with a 4 mm full-width-half-maximum Gaussian smoothing kernel, and high-pass temporal filtering by removal of linear trends and temporal components below 3 cycles per run.

During fMRI participants viewed a full-field (14.5° × 19.3°) stimulus that alternated between periods of moving dots and stationary dots (Fig. 1A). Each of 8 moving-stationary cycles lasted 28 s. The stimulus was comprised of 400 dots (each dot was 0.05° in diameter) that appeared at random locations along the outer edge and then moved toward the central fixation point with 100% coherence and a velocity of 5°/s. Participants were instructed to maintain central fixation and, during motion periods, press a button when they detected a brief whole-field slowdown (which occurred twice per motion period).

An individual participant general linear model analysis was conducted, where significant motion related activity ($p < 0.01$) was identified by contrasting periods of moving dots vs. stationary dots [26,30] and then projected onto each participant's cortical surface representation. For each hemisphere of a given participant, the precise location of motion processing sub-region MT was identified using functional, anatomic, and meta-analytic constraints: (1) MT was constrained to be within the significant motion related activity on the cortical surface, (2) MT was constrained to be within the posterior bank of the ascending limb of the inferior temporal sulcus [5,10,15], and (3) MT was constrained to be within the range of motion processing region coordinates produced by a meta-analysis of the literature [19]. In each hemisphere, these joint constraints yielded the specific locus of MT that was subsequently targeted during TMS (Fig. 1B).

The BrainVoyager TMS Neuronavigation System was used for TMS positioning relative to the target location (for details, see [18,22,28]). In brief, landmarks on the head and TMS coil were identified in both external space (using a digitizer pen) and BrainVoyager space, and co-registered. Ultrasound transmitters affixed to the head and TMS coil emitted signals that were picked up by a receiving sensor device in external space to precisely track the location of the TMS coil in relation to the head (and underlying cortical surface) in BrainVoyager space. For a given hemisphere, before TMS commenced, the MT target location was placed on the cortical surface (Fig. 1B, red sphere within the white square). To temporarily disrupt MT in each hemisphere, a Magstim Rapid$^2$ system with a Double 70 mm Coil (The Magstim Company Ltd., Carmarthenshire, Wales) was used to apply 1-Hz repetitive TMS at 70% of maximum output for 10 min. Of importance, these TMS parameters (i.e., 1-Hz stimulation for 10 min) constitute a standard TMS protocol that has been shown to impair processing in the targeted cortical region for at least 10 min following the offset of stimulation [16]. The coil was positioned to be approximately perpendicular to the head surface with minor adjustment to ensure the TMS beam was focused at the target point (MT) on the posterior bank of the ascending limb of the inferior temporal sulcus. Stimulation of the anterior bank of the ascending limb of the inferior temporal sulcus, the known location of motion processing sub-region MST [10,15] was specifically avoided. The TMS cable was oriented posteriorly and downward 45° from horizontal. During TMS, participants made odd/even judgements to black digits (ranging from 0 to 9) presented at fixation on a gray background (each digit was presented for 1 s followed by a 1–10 s fixation period). For each participant, there was a 30 minute break between TMS of each hemisphere. The initial hemisphere of TMS was randomly assigned for each participant and behavioral testing was completed within 7 min of TMS offset.

The spatial attention stimulus was composed of moving dots within two squares, one in each hemifield, rotated 30° from horizontal (Fig. 1C). Each square had a 5° edge length with the nearest corner 2° from the central fixation point, and contained 320 dots (each dot was 0.06° in diameter) which moved with 70% coherence at a velocity of 6°/s. To avoid perceptual grouping, dots in the left square moved downward and dots in the right square moved upward. A brief increase in dot speed within the attended hemifield (i.e., a shift target) cued participants to shift attention to the square in the opposite visual field (and press the corresponding 'shift' key) and sustain attention at this new location. A brief decrease in dot speed within the attended hemifield (i.e., a detect target) cued participants to press the 'detect' key. Each participant completed two runs during the TMS session (i.e., one run following each stimulation period) lasting 145–150 s where dot speed changes occurred at random times every 2–10 s within each hemifield (dot speed increases or decreases occurred with equal probability; the total number of possible detect targets was 10.98 ± 0.89 and 12.02 ± 0.81 in the left and right visual field, respectively). Eight of the ten participants also completed two runs with no TMS, which served as a control level of behavioral performance. Percent detection was calculated based on the number of detect targets occurring within the attended hemifield. One-tailed $t$-tests were employed because temporary disruption of MT was expected to preferentially impair detection of targets in the contralateral visual field (only $p$-values <0.05 were considered significant).

TMS to left MT produced a significant impairment in detection of targets in the contralateral versus ipsilateral visual field (Fig. 1D, bars 1, 2; $t(9) = 1.86$, $p < 0.05$). Performance following TMS was compared to no TMS (control) performance to assess whether disruption of left MT impaired contralateral target detection, facilitated ipsilateral target detection, or produced both of these effects. Contralateral target detection following TMS to left MT was significantly lower than no TMS performance (Fig. 1D, bars 2, 3; $t(7) = 2.59$, $p < 0.05$), and ipsilateral target detection following TMS to left MT was also significantly lower than no TMS performance (Fig. 1D, bars 1, 3; $t(7) = 3.36$, $p < 0.01$). Together, these results demonstrate that TMS to left MT impaired contralateral target detection and did not facilitate ipsilateral target detection (which would have been manifested by higher ipsilateral performance following TMS as compared to no TMS performance; the opposite was observed).

TMS to right MT did not produce a significant difference between contralateral versus ipsilateral target detection (Fig. 1D, bars 4, 5; $t(8) < 1$), and appeared to produce an impairment in both visual fields as contralateral and ipsilateral performance did not significantly differ from contralateral (impaired) performance following TMS to left MT (Fig. 1D, bars 2, 4, 5; $F(2,16) < 1$). Moreover, no TMS target detection was significantly greater than ipsilateral and contralateral target detection following TMS to right MT (Fig. 1D, bars 4, 5, 6; $t(6) = 2.22$, $p < 0.05$). These results suggest that temporary disruption of right MT produced both a contralateral and ipsilateral

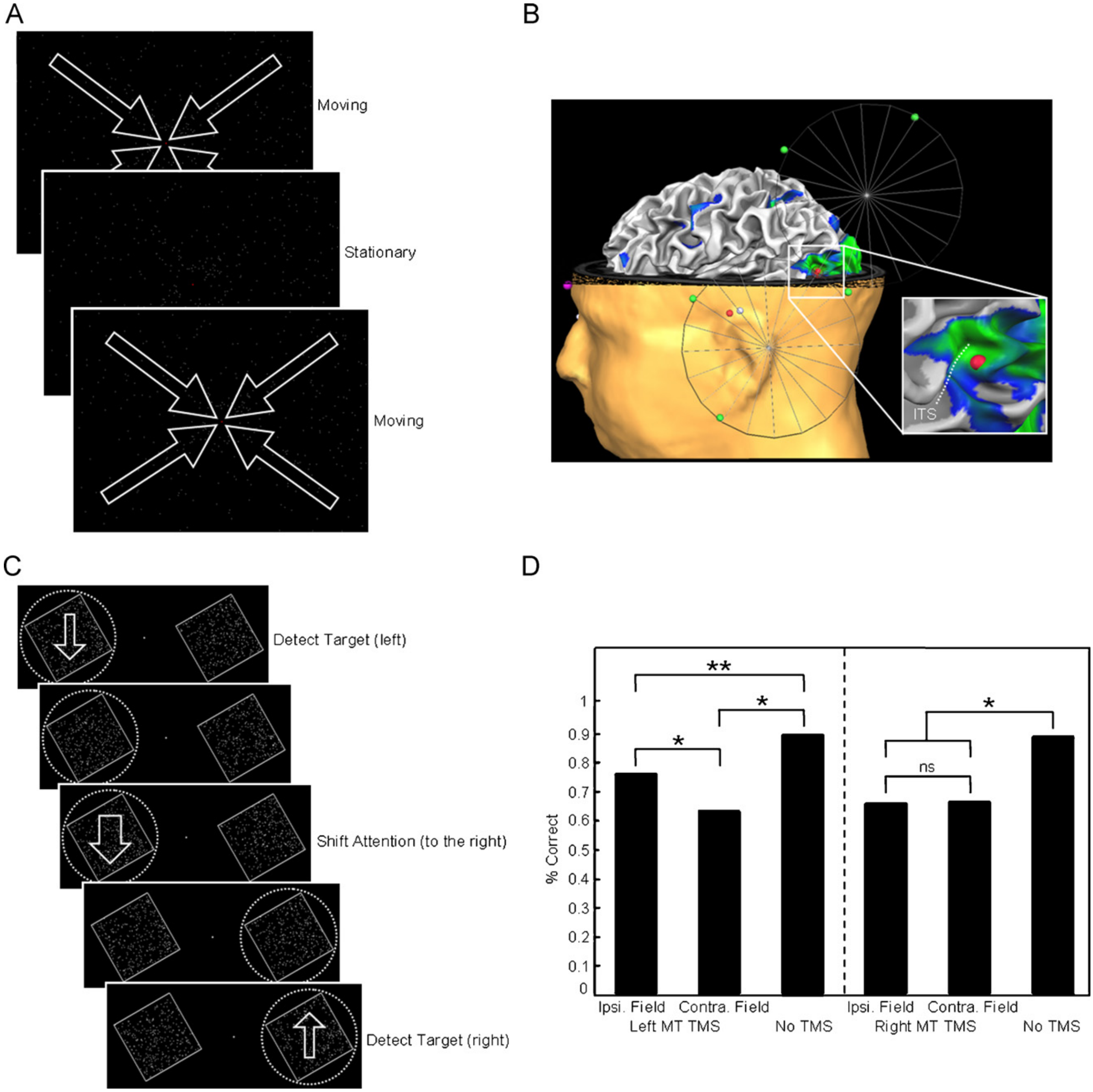


**Fig. 1.** (A) The motion localizer stimulus alternated between periods of moving and stationary dots (arrows illustrate movement and were not present during the experiment). (B) fMRI guided neuronavigation. To the left, a representative participant's head surface and left hemisphere cortical surface with motion related activity (gyri and sulci are shown in light and dark gray, respectively; more significant activity is shown in green). The TMS coil is delineated by two wireframe wheels. TMS was applied to motion processing region MT, marked by the red sphere on the posterior bank of the ascending limb of the inferior temporal sulcus (ITS; magnified MT region is shown to the right with a dotted line tracing the fundus). (C) During the spatial attention protocol, participants shifted attention between moving dots in the left or right hemifield when dots in the attended hemifield briefly increased speed (wide arrow) or pressed a key when dots in the attended hemifield briefly decreased speed, a detect target (narrow arrows; dotted circles illustrate the locus of attention and were not present during the experiment). (D) Percent detection of targets in the ipsilateral (ipsi.) visual field following TMS, contralateral (contra.) visual field following TMS, and no TMS (control) performance separated by hemisphere of TMS stimulation (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ns = not significant). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

impairment in target detection, in contrast to temporary disruption of left MT which produced a preferential impairment in contralateral target detection.

*Experiment 2*: The previous experiment used an attention task, where participants shifted attention between hemifields and detected targets in the attended hemifield. Because such tasks involve both focused attention to and perceptual processing of a particular spatial location [30], it is uncertain whether the preceding contralateral motion effects were due to impaired visual attentional processing or impaired visual perceptual processing. To address this, a motion detection task was employed to determine whether TMS to MT would impair perceptual processing without an explicit attentional component. Moreover, single-pulse TMS was used to test whether a motion processing impairment would be observed using a different TMS protocol, and a color detection task was used to ensure that the effects were specific to motion (as it could be argued that TMS of a more posterior extrastriate region associated with contralateral, but not motion specific, visual processing might have produced the effects in Experiment 1).

Unless otherwise stated, the experimental procedure was identical to Experiment 1. Four participants from the Boston College community with normal or corrected-to-normal vision took part

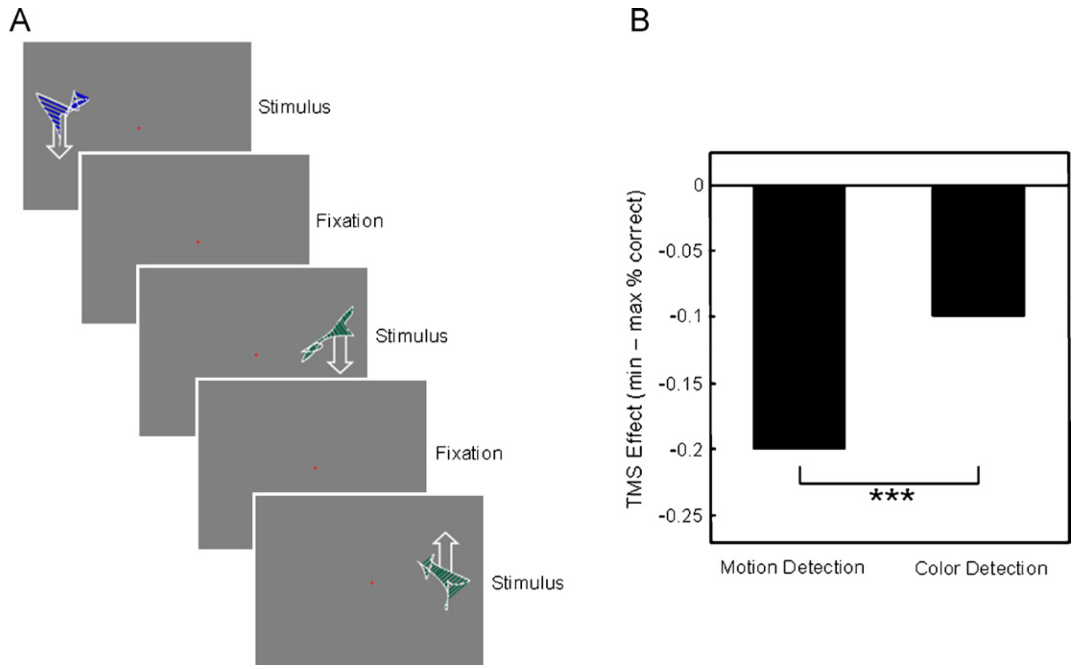


**Fig. 2.** (A) Stimulus for the motion detection and color detection tasks. (B) TMS effect (minimum minus maximum percent correct) for the motion detection task and color detection task (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ns = not significant).

in the study (two had participated in Experiment 1). One participant was excluded due to chance performance, such that three participants were included in the final analysis (1 female, age range 21–39 years). The TMS and fMRI protocols were approved by the Boston College and Massachusetts General Hospital Institutional Review Boards, respectively. Informed consent was obtained before the experiment commenced.

The identical stimulus protocol was used for both a motion detection task and a color detection task (Fig. 2A). On each trial, an abstract shape with a white outline and either blue or green internal lines was presented to the left or right of fixation and moved briefly up or down, followed by a 1.4 s period of fixation (for a detailed description of shape construction see [25]). Internal line color, spatial location, and movement direction were randomly determined, with the constraint that all conditions occurred equally often in each run. Shapes were never repeated. Each shape moved vertically across the horizontal meridian, traversing 0.21° with a velocity of 3.4–6.9°/s (velocity was adjusted for each participant such that performance was approximately 75% correct). After practicing the tasks, each participant completed one motion detection run and one color detection run during TMS. In motion detection runs, participants were instructed to maintain central fixation and press one of two buttons to classify each shape as moving up or down (and were instructed to ignore color information). In color detection runs, participants were instructed to maintain central fixation and press one of two buttons to classify each shape as blue or green (and were instructed to ignore motion information).

For each participant, the MT target location was identified using the same procedure as described in Experiment 1 (although in this experiment, a single hemisphere of stimulation was randomly selected; 1 right hemisphere). TMS was applied at 70% of maximum output using a single-pulse TMS protocol, where on each trial the stimulus computer triggered the TMS system to deliver a pulse at a specific time following stimulus onset (with the aim of disrupting processing in MT at that time). TMS pulses occurred in 17 ms increments within 68–218 or 98–248 ms after stimulus onset, and were time-locked to the vertical refresh rate (60 Hz). Each run consisted of 200 trials (20 trials at each of 10 pulse times). Analysis was restricted to 98–201 ms after stimulus onset, the expected time period of impaired motion processing following single-pulse TMS [17], to minimize the contribution of noise in the analysis. The TMS effect for both tasks was computed as the minimum minus the maximum percent correct (see supplementary Fig. 1). One-tailed $t$-tests were employed as temporary disruption of MT was expected to preferentially impair detection of motion targets (only $p$-values <0.05 were considered significant).

TMS to MT produced a significantly greater impairment in motion detection than color detection (Fig. 2B, task, motion and color, by TMS effect interaction $p < 0.001$; Levene's test for homogeneity of variance, both task $p$-values > 0.20). This result was not due to differences in task difficulty as performance did not differ between tasks at the first timepoint ($t(2) < 1$), a measure of baseline performance.

Consistent with the Experiment 1 right hemisphere TMS findings, TMS to MT impaired motion detection in both the contralateral visual field ($t(2) = 11.00$, $p < 0.01$) and the ipsilateral visual field ($t(2) = 7.00$, $p < 0.01$). There was no significant spatial location (contralateral and ipsilateral) by TMS effect interaction ($p = 0.09$).

In Experiment 1, 1 Hz TMS to left MT preferentially impaired motion processing in the contralateral visual field during an attention task. In Experiment 2, single-pulse TMS to MT impaired motion processing to a greater degree than color processing during a perception task. Taken together, these results suggest that TMS to MT can produce contralateral and feature-specific motion processing impairments, arguing against the possibilities that MST, which processes both contralateral and ipsilateral motion, was targeted or that a motion and color processing region was targeted. Moreover, the results of Experiment 2 illustrated that TMS to MT could disrupt perceptual processing (as attention and perception effects were confounded in Experiment 1).

In a recent case study [19], we reported a patient with a putative left MT+ lesion who was preferentially impaired at motion processing tasks in the contralateral visual field, as in the present Experiment 1, with minimal fMRI motion perception or motion attention effects in this region. These impairments occurred primarily in the contralesional visual field suggesting the lesion included sub-region MT. However, the extent of the lesion was uncertain and may have included adjacent motion sensitive region V3A. As such, the results of Experiment 1 are the first, to our knowledge, where definitive disruption of MT impaired motion processing in the contralateral greater than ipsilateral visual field.

It is important to highlight that TMS to MT impaired contralateral and ipsilateral motion processing in both experiments, which suggests disruption of MT may have transferred to more anterior sub-region MST. This is an inherent weakness of the current study that may have methodological implications for future fMRI-guided TMS research. The present results suggest that using fMRI localization to guide stimulation may be limited to selectively target MT and identify its role in contralateral motion processing. Silvanto and Muggleton [24] differentially targeted MT+ by employing a visual adaptation paradigm with motion properties that were selectively processed by this region. If such a technique is used in conjunction with localization procedures, as in the present study, it could enhance TMS accuracy and better guide stimulation of distinct neural populations within a single cortical area (e.g., sub-region MT or MST within motion processing region MT+).

Of direct relevance to our aim, the present results showed that selective disruption of MT, the sub-region of MT+ that preferentially processes contralateral motion, can impair contralateral and feature-specific motion processing. These findings complement previous neuroimaging studies that have associated motion perception and motion attention with sub-region MT [1,6,10,12,15,20,26,27]. Of primary importance, building on previous MT+ TMS studies [4,9,18,22,28], the present findings indicate sub-region MT is necessary for motion processing.

## Acknowledgement

Supported by NSF grant BCS0745880.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neulet.2010.12.057.

## References

[1] K. Amano, B.A. Wandell, S.O. Dumoulin, Visual field maps, population receptive field sizes, and visual field coverage in the human MT+ complex, J. Neurophysiol. 102 (2009) 2704–2718.
[2] S. Anand, J.D. Olson, J.R. Hotson, Tracing the timing of human analysis of motion and chromatic signals from occipital to temporo-parieto-occipital cortex: a transcranial magnetic stimulation study, Vision Res. 38 (1998) 2619–2627.
[3] A. Antal, M.A. Nitsche, W. Paulus, Transcranial magnetic and direct stimulation of the visual cortex, Suppl. Clin. Neurophysiol. 56 (2003) 291–304.
[4] L. Battelli, G.A. Alvarez, T. Carlson, A. Pascual-Leone, The role of the parietal lobe in visual extinction studied with transcranial magnetic stimulation, J. Cogn. Neurosci. 21 (2008) 1946–1955.
[5] M.S. Beauchamp, N.E. Yasar, N. Kishan, T. Ro, Human MST but not MT responds to tactile stimulation, J. Neurosci. 27 (2007) 8261–8267.
[6] H.G.T. Becker, M. Erb, T. Haarmeier, Differential dependency on motion coherence in subregions of the human MT+ complex, Eur. J. Neurosci. 28 (2008) 1674–1685.
[7] G. Beckers, V. Hömberg, Cerebral visual motion blindness: transitory akinetopsia induced by transcranial magnetic stimulation of human area V5, Proc. Biol. Sci. 249 (1992) 173–178.
[8] G. Beckers, S. Zeki, The consequences of inactivating areas V1 and V5 on visual motion perception, Brain 118 (1995) 49–60.
[9] M.P. Burton, D.J. McKeefry, B.T. Barrett, C. Vakrou, A.B. Morland, Disruptions to human speed perception induced by motion adaptation and transcranial magnetic stimulation, Eur. J. Neurosci. 30 (2009) 1989–1998.
[10] S.P. Dukelow, J.F. DeSouza, J.C. Culham, A.V. van den Berg, R.S. Menon, T. Vilis, Distinguishing subregions of the human MT+ complex using visual fields and pursuit eye movements, J. Neurophysiol. 86 (2001) 1991–2000.
[11] A. Ellison, A.R. Lane, T. Schenk, The interaction of brain regions during visual search processing as revealed by transcranial magnetic stimulation, Cereb. Cortex 17 (2007) 2579–2584.
[12] J. Goossens, S.P. Dukelow, R.S. Menon, T. Vilis, A.V. van den Berg, Representation of head-centric flow in the human motion complex, J. Neurosci. 26 (2006) 5616–5627.
[13] B.M. Harvey, O.J. Braddick, A. Cowey, Similar effects of repetitive transcranial magnetic stimulation of MT+ and a dorsomedial extrastriate site including V3A on pattern detection and position discrimination of rotating and radial motion patterns, J. Vis. 10 (2010) 1–15.
[14] J.R. Hotson, S. Anand, The selectivity and timing of motion processing in human temporo-parieto-occipital and occipital cortex: a transcranial magnetic stimulation study, Neuropsychology 37 (1999) 169–179.
[15] A.C. Huk, R.F. Dougherty, D.J. Heeger, Retinotopy and functional subdivision of human areas MT and MST, J. Neurosci. 22 (2002) 7195–7205.
[16] S.M. Kosslyn, A. Pascual-Leone, O. Felician, S. Camposano, J.P. Keenan, W.L. Thompson, G. Ganis, K.E. Sukel, N.M. Alpert, The role of area 17 in visual imagery: convergent evidence from PET and rTMS, Science 284 (1999) 167–170.
[17] R. Laycock, D.P. Crewther, P.B. Fitzgerald, S.G. Crewther, Evidence for fast signals and later processing in human V1/V2 and V5/MT+: a TMS study of motion perception, J. Neurophysiol. 98 (2007) 1253–1262.
[18] D.J. McKeefry, M.P. Burton, C. Vakrou, B.T. Barrett, A.B. Morland, Induced deficits in speed perception by transcranial magnetic stimulation of human cortical areas V5/MT+ and V3A, J. Neurosci. 28 (2008) 6848–6857.
[19] L.R. Moo, B.C. Emerton, S.D. Slotnick, Functional MT+ lesion impairs contralateral motion processing, Cogn. Neuropsychol. 25 (2008) 677–689.
[20] S. Ohlendorf, A. Sprenger, O. Speck, S. Haller, H. Kimmig, Optic flow stimuli in and near the visual field centre: a group fMRI study of motion sensitive regions, PLoS One 3 (2008) 1–7.
[21] S. Raiguel, M.M. Van Hulle, D.K. Xiao, V.L. Marcar, G.A. Orban, Shape and spatial distribution of receptive fields and antagonistic motion surrounds in the middle temporal area (V5) of the macaque, Eur. J. Neurosci. 7 (1995) 2064–2082.
[22] A.T. Sack, A. Kohler, D.E.J. Linden, R. Goebel, L. Muckli, The temporal characteristics of motion processing in hMT/V5+: combining fMRI and neuronavigated TMS, Neuroimage 29 (2006) 1326–1335.
[23] J. Silvanto, N. Lavie, V. Walsh, Double dissociation of V1 and V5/MT activity in visual awareness, Cereb. Cortex 15 (2005) 1736–1741.
[24] J. Silvanto, N.G. Muggleton, Testing the validity of the TMS state-dependency approach: targeting functionally distinct motion-selective neural populations in visual areas V1/V2 and V5/MT+, Neuroimage 40 (2008) 1841–1848.
[25] S.D. Slotnick, D.L. Schacter, A sensory signature that distinguishes true from false memories, Nat. Neurosci. 7 (2004) 664–672.
[26] S.D. Slotnick, S. Yantis, Common neural substrates for the control and effects of visual attention and perceptual bistability, Cogn. Brain Res. 24 (2005) 97–108.
[27] A.T. Smith, M.B. Wall, A.L. Williams, K.D. Singh, Sensitivity to optic flow in human cortical areas MT and MST, Eur. J. Neurosci. 23 (2006) 561–569.
[28] L.K. Stevens, P.V. McGraw, T. Ledgeway, D. Schluppeck, Temporal characteristics of global motion processing revealed by transcranial magnetic stimulation, Eur. J. Neurosci. 30 (2009) 2415–2426.
[29] L. Stewart, L. Battelli, V. Walsh, A. Cowey, Motion perception and perceptual learning studied by magnetic stimulation, Electroencephalogr. Clin. Neurophysiol. Suppl. 51 (1999) 334–350.
[30] P.P. Thakral, S.D. Slotnick, The role of parietal cortex during sustained visual spatial attention, Brain Res. 1302 (2009) 157–166.
[31] B. Thompson, C. Aaen-Stockdale, L. Koski, R.F. Hess, A double dissociation between striate and extrastriate visual cortex for pattern motion perception revealed using rTMS, Hum. Brain Mapp. 30 (2009) 3115–3126.
[32] R.B. Tootell, J.D. Mendola, N.K. Hadjikhani, A.K. Liu, A.M. Dale, The representation of the ipsilateral visual field in human cerebral cortex, Proc. Natl. Acad. Sci. U. S. A. 195 (1998) 818–824.
[33] V. Walsh, A. Ellison, L. Batelli, A. Cowey, Task-specific impairments and enhancements induced by magnetic stimulation of human visual area V5, Proc. Biol. Sci. 265 (1998) 537–543.
[34] J.D.G. Watson, R. Myers, R.S.J. Frackowiak, J.V. Hajnal, R.P. Woods, J.C. Mazziotta, S. Shipp, S. Zeki, Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging, Cereb. Cortex 3 (1993) 79–94.