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RESEARCH ARTICLE

Global versus local: double dissociation between MT+ and V3A in motion processing revealed using continuous theta burst transcranial magnetic stimulation

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Abstract The functional properties of motion selective areas in human visual cortex, including V3A, MT+, and intraparietal sulcus (IPS) are not fully understood. To examine the functional specialization of these areas for global and local motion processing, we used off-line, neuronavigated, continuous theta burst (cTBS) transcranial magnetic stimulation to temporarily alter neural activity within unilateral V3A, MT+, and IPS. A within-subjects design was employed and stimulation sessions were separated by at least 24 h. In each session, subjects were asked to discriminate the global motion directions of successively presented random dot kinematograms (RDKs) before and after cTBS. RDKs were presented at either 100 or 40 % coherence in either the left or right visual field. We found that V3A stimulation selectively impaired discrimination of 100 % coherent motion, while MT+ stimulation selectively impaired discrimination of 40 % coherent motion. IPS stimulation impaired discrimination of both motion stimuli. All cTBS effects were specific to stimuli presented contralaterally to the stimulation site and vertex stimulation had no effect. The double dissociation between the cTBS effects on MT+ and V3A indicates distinct roles for these two regions in motion processing. Judging the direction of 100 % coherent motion can rely on local motion processing because every dot moves in the same direction. However, judging the global direction of 40 % coherent motion requires global processing. Thus, our results suggest separate, parallel processing of local and global motion in V3A and MT+, respectively, with the outputs of these two areas being combined within the IPS.

Keywords Visual motion · Transcranial magnetic stimulation (TMS) · Continuous theta burst stimulation (cTBS) · V3A · MT+ · IPS

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Introduction

Global motion perception, which requires the integration of motion signals across time and space, is a critical aspect of our daily life. We often have to judge the global direction of a group of objects, with members of the group moving in different directions (e.g., a flock of birds, a crowd of people). Furthermore, averaging motion signals across space can help to overcome the poor reliability of sparsely distributed local motion signals (Braddick 1993). Psychophysical

studies of global motion often employ random dot kinematograms (RDKs), which are constructed from a population of signal dots moving in a common direction and a population of noise dots, which move in random directions. The coherence of the motion is manipulated by varying the proportion of signal to noise from 100 % signal (fully coherent) to 100 % noise (incoherent). Psychophysical and neurophysiological studies have indicated that perceiving the direction of partially coherent motion or discriminating coherent from incoherent motion reflects global rather than local motion processing (Newsome and Pare 1988; Scase et al. 1996; Braddick et al. 2001).

Motion information is represented in many visual cortical areas (Dupont et al. 1994; Tootell et al. 1995, 1997; McKeefry et al. 1997; Sunaert et al. 1999; Braddick et al. 2001); however, it is generally acknowledged that dorsal extrastriate area MT+ plays a prominent role in the cortical analysis of visual motion processing. Neurons in this area can integrate multiple local motion directions and signal global motion (Britten et al. 1993; Rust et al. 2006). Furthermore, lesions of MT lead to impaired global motion perception (Newsome and Pare 1988; Shipp et al. 1994; Rizzo et al. 1995; Vaina et al. 2005). In humans, V3A also appears to be specialized for motion processing (Tootell et al. 1997; Orban et al. 2003; Bartels et al. 2008; McKeefry et al. 2008). Human V3A exhibits a high motion direction selectivity (Cornette et al. 1998; Huk et al. 2001; Moutoussis et al. 2005; Kamitani and Tong 2006; McKeefry et al. 2008; Serences et al. 2009) and has a stronger response to coherent motion than incoherent motion (Rees et al. 2000; Braddick et al. 2001). Besides MT+ and V3A, the intraparietal sulcus (IPS) has also been implicated in visual motion processing, especially in motion decision making (Tootell et al. 1995; Sunaert et al. 1999; Braddick et al. 2001; Konen and Kastner 2008; Cardin and Smith 2010; Helfrich et al. 2013). Neurons in macaque IPS receive strong projections from MT and MST (Lewis and Van Essen 2000), and microstimulation of this area affects decision making in a motion discrimination task (Hanks et al. 2006). Human IPS is partially homologous with monkey IPS (Orban et al. 2004; Grefkes and Fink 2005) and consists of a continuous band of topographically organized parietal areas (Swisher et al. 2007; Wandell et al. 2007; Silver and Kastner 2009).

Although a series of motion-sensitive areas have been identified within the human dorsal extrastriate visual cortex, the specific functional properties of these regions remain largely unknown. Previous studies have demonstrated that transcranial magnetic stimulation (TMS) over V3A or MT+ can disrupt motion perception (Beckers and Homberg 1992; Hotson et al. 1994; Beckers and Zeki 1995; McKeefry et al. 2008; Thompson et al. 2009; Harvey et al. 2010). Nevertheless, no dissociable TMS effect has been observed between these two regions. On the other hand, the TMS effect over human IPS on motion perception still remains elusive (Cowey et al. 2006). Do these regions have distinct roles in motion processing? What are their relationships to the cortical hierarchy of motion processing?

This study aimed to examine the causal contributions made by visual areas MT+, V3A, and IPS to global and local motion processing. To this end, we deployed off-line continuous theta burst stimulation (cTBS) to transiently attenuate normal functioning of these areas (Huang et al. 2005; van Kemenade et al. 2012a) and tested motion discrimination for different motion coherence conditions. Functional magnetic resonance imaging (fMRI) mapping was used to localize V3A, MT+, and IPS in individual subjects and guide cTBS delivery. The vertex was also targeted as a control site. Motion direction discrimination thresholds were compared before and after cTBS and stimuli were presented contralateral or ipsilateral to the simulation site at two motion coherence levels. For the 100 % coherent stimuli, motion direction discrimination could be performed using only local motion signals because every dot moved in the same direction. However, for the 40 % coherent stimuli, global processing was required to form a coherent motion perception.

Methods

Participants

Eight neurologically healthy participants (four females, age range, 20–28 years) took part in this study. All participants had normal or corrected-to-normal vision and were right-handed. All procedures were approved by the human subject review committee of Peking University, and participants provided fully informed consent. There were no adverse reactions to the TMS.

Psychophysical motion direction discrimination task

The stimuli were presented on an IIYAMA HM204DT 22 inch monitor with a refresh rate of 100 Hz and a resolution of 1,024 × 768 pixels using MATLAB (Mathworks, Natrick, MA) and the Psychtoolbox3 (Brainard 1997; Pelli 1997). Participants viewed the stimuli at a distance of 60 cm with their heads stabilized by a chin and head rest, and were asked to fixate a small white dot presented at the center of the screen throughout the experiment. The stimuli were RDKs consisting of 400 dark dots moving at a velocity of 10°/s within a virtual circular area subtending 9° in diameter. The center of the aperture was positioned 9° horizontally to the left or right of the central fixation point (see Fig. 1). Each dot had a diameter of 0.1° and luminance of 0.021 cd/m^2 against an 11.55 cd/m^2 background. In the

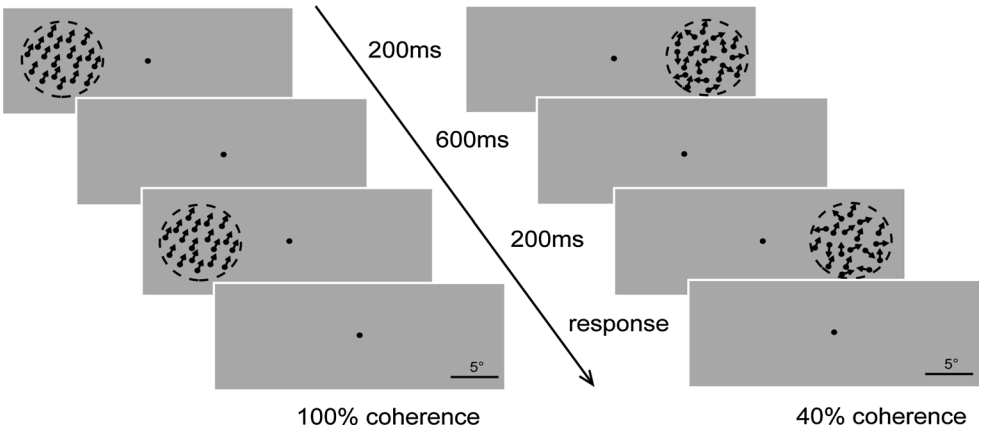

Fig. 1 Schematic description of a two-alternative force choice (2AFC) trial in a QUEST staircase for measuring motion direction discrimination thresholds using random kinematograms (RDKs). RDKs were presented at either 100 % or 40 % coherence in either the *left* or *right* visual field. Subjects were asked to judge the direction of the second RDK relative to the first one (clockwise or counterclockwise)

100 % motion coherence condition, all dots moved in the same direction. In the 40 % motion coherence condition, 40 % dots were assigned to be signal, while the rest of dots were assigned to be noise. Signal and noise labels were randomly assigned every 10 ms. Noise dots were plotted at random positions creating local motion signals of varying direction and speed (Scase et al. 1996). A QUEST staircase procedure was used to estimate 75 % correct motion direction discrimination thresholds. For each TMS site, subjects completed four QUEST staircases of 40 trials (Watson and Pelli 1983) for each coherence and position (i.e., left or right visual field) condition before and after TMS. Each trial consisted of two stimulus presentations lasting 200 ms with a 600 ms interstimulus interval. One stimulus had a motion direction of 22.5° and the other 22.5° + $\Delta\theta$ from vertical. Both stimuli in a trial had the same coherence and were presented in the same position. The order of the two motion directions was randomized across trials. Subjects were asked to make a two-alternative forced-choice (2AFC) judgment of whether the change in motion direction from the first to the second RDK was clockwise or counterclockwise. The order of the staircases was randomized.

MR data acquisition

Scanning was performed using a 3 Tesla Siemens Trio scanner with a 12-channel phased array head coil. Blood-oxygenation-level-dependent (BOLD) signals were measured with an EPI sequence (33 axial slices, repetition time (TR) = 2 s, echo time (TE) = 30 ms, voxel size = 3 × 3 × 3 mm^3, and no interslice gap). A high-resolution 3D structural data set (T1-weighted MPRAGE, 1 × 1 × 1 mm^3 resolution) was acquired in the same session.

Identification of visual areas responsive to motion

For each subject, borders of retinotopic visual areas (V1, V2, V3, and V3A) were defined using a standard phase-encoded method (Sereno et al. 1995; Engel et al. 1997). An independent block-design run was conducted to localize motion-sensitive areas—V3A, MT+, and IPS. In this run, 12-s moving dot blocks were interleaved with 12-s stationary dot blocks. In the moving dot blocks, the stimulus was identical to that in the psychophysical experiment except that each dot moved in a random direction. The dots traveled back and forth, alternating direction once per second. The stimulus was presented in the left visual field in half of the moving dot blocks, and in the right visual field in the other half.

The fMRI data were analyzed with the BrainVoyager QX software (Brain Innovation). Preprocessing of the data included three-dimensional motion correction, linear trend removal, and high-pass filtering at 0.015 Hz. The statistical analysis of the BOLD signals was performed using a general linear model. To stimulate the regions that responded specifically to the motion stimuli in the contralateral visual field, the voxels in V3A, MT+, and IPS exhibiting a significantly stronger response to contralateral than ipsilateral moving dots were identified. The IPS voxels were located in the medial dorsal intraparietal sulcus, which is also referred to as IPS2 (Swisher et al. 2007; Wandell et al. 2007).

TMS

Continuous theta burst stimulation was delivered through a MagStim Super Rapid^2 stimulator (MagStim, Whitland, UK) and a double 70-mm figure-of-eight coil. A train of 600 pulses, 3 pulses at 50 Hz delivered every 200 ms, was delivered at a 100 % of each participant's active motor threshold (AMT) intensity. AMT was determined individually in the tonically active first dorsal interosseous (FDI) muscle as the stimulation intensity that evoked a motor-evoked potential of at least 50 μV in five of ten consecutive trials using biphasic single-pulse TMS over contralateral motor cortex. The range of thresholds was 44–50 % of the maximum stimulator output. The off-line cTBS protocol was chosen as it has been found to result

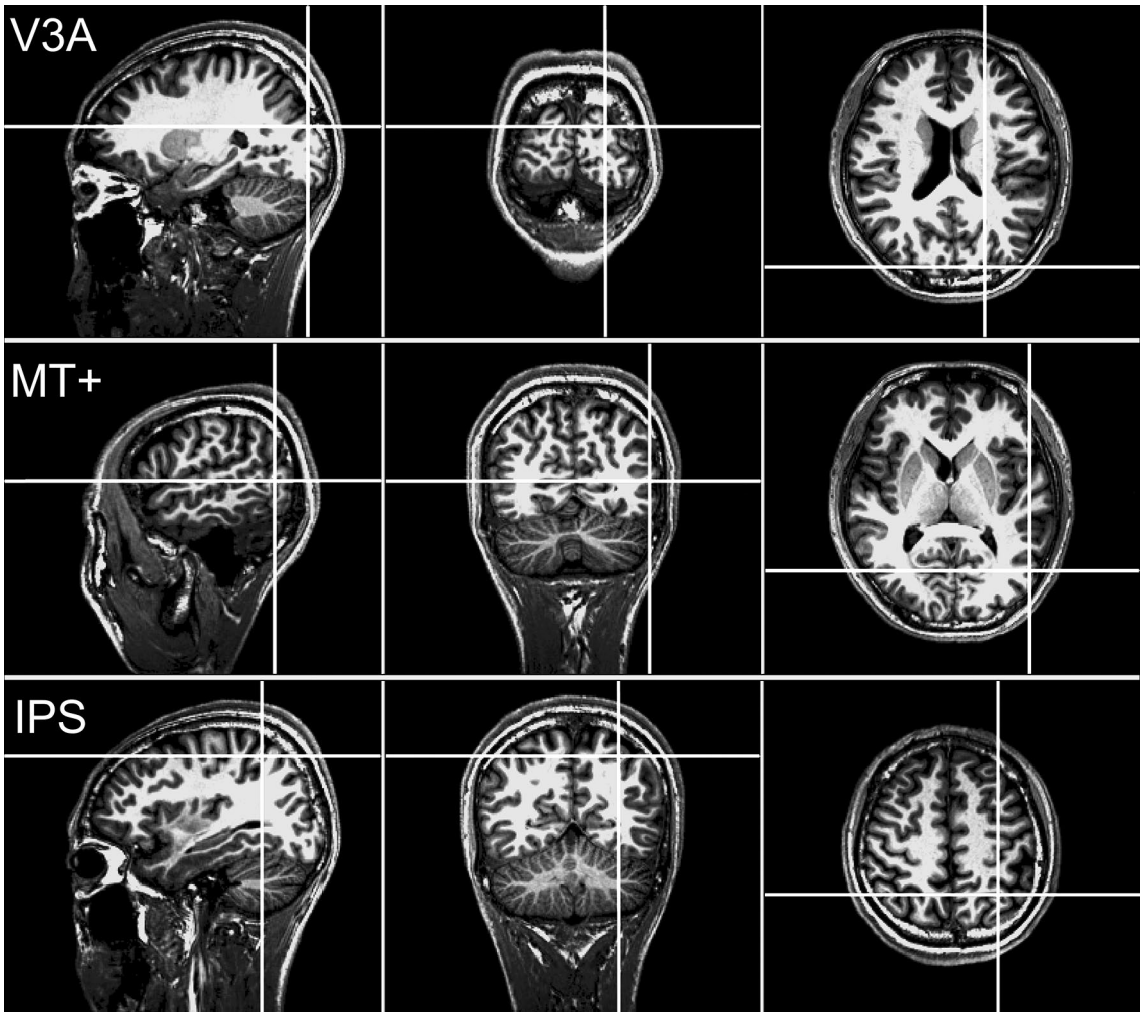

Fig. 2 TMS stimulation sites—V3A (*top row*), MT+ (*middle row*), and IPS (*bottom row*). The crosses indicate the voxels in the three motion-sensitive areas that were most significantly activated by the motion localizer in a representative subject

in cortical suppression for up to 60 min (Huang et al. 2005; Allen et al. 2007), which was enough for all subjects to complete the behavioral tasks. cTBS was guided using participant specific structural and functional MRI data and the Visor2 neuro-navigation system (Advanced Neuro Technology, The Netherlands). The stimulation sites in V3A, MT+, and IPS in the same hemisphere were the voxels exhibiting the strongest BOLD activation (contralateral vs. ipsilateral) in each area (see Fig. 2). The coil was held over the scalp tangentially with the handle directing posterior toward the occiput parallel to the subject's spine. The position of the coil was monitored through the course of the 40-s cTBS protocol. The vertex, the location halfway between the inion and the nasion and halfway between the intertragal notches, served as the control site. The stimulation order was counterbalanced across subjects, and each session was separated by at least 24 h.

Results

In each session, subjects were asked to perform a motion direction discrimination task before and after cTBS. Thresholds were measured for two motion coherence levels (100 or 40 %) at two stimulus locations (left and right visual field). The cTBS effect was evaluated by computing the difference between the motion direction discrimination thresholds before and after cTBS ($threshold_{post}$–$threshold_{pre}$). A difference larger than zero indicated a disruption of motion discrimination, and a difference smaller than zero indicated a facilitation of motion discrimination.

We examined the cTBS effect across all conditions using a three-way repeated-measures ANOVA, with stimulation site (V3A, MT+, IPS), motion coherence (40, 100 %), and stimulus position (contralateral, ipsilateral to the stimulated site) as independent factors. A significant interaction was revealed ($F(2,14) = 9.893$, $P < 0.01$), indicating that the

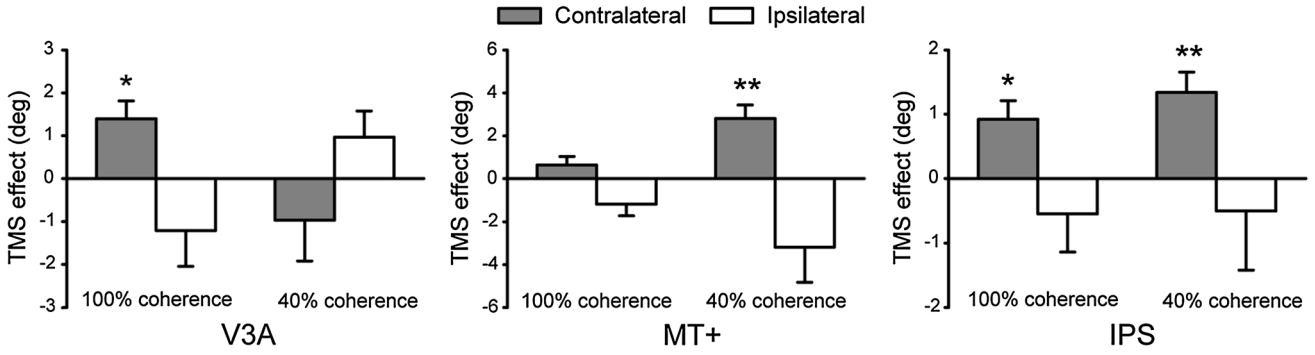

Fig. 3 TMS effects over V3A, MT+, and IPS on motion direction discrimination. Motion discrimination thresholds were measured for two coherence levels (100 or 40 %) at two locations (ipsilateral and contralateral visual fields). TMS effects were quantified by computing the difference between the motion direction discrimination thresholds before and after cTBS ($threshold_{post}$–$threshold_{pre}$). A difference larger than zero indicated a disruption of motion discrimination and a difference smaller than zero indicated a facilitation of motion discrimination. The *asterisks* indicate that the TMS effect is significant (*$P < 0.05$; **$P < 0.01$). *Error bars* denote 1 SEM

effect of cTBS on direction discrimination was modulated by motion coherence, stimulus position, and stimulation site. Then, we performed a two-way repeated-measures ANOVA for each stimulation site. When V3A was stimulated (Fig. 3a), there was a significant interaction between motion coherence and stimulus position [$F(1, 7) = 10.976$, $P < 0.05$]. The cTBS effect was only significant when 100 % coherence stimuli were presented in the contralateral visual field [one-sample t test, $t(7) = 3.351$, $P < 0.05$]. A different pattern occurred when MT+ was stimulated (Fig. 3b). The interaction between motion coherence and stimulus position was also significant [$F(1, 7) = 7.168$, $P < 0.05$]. However, the cTBS effect was only significant when 40 % coherent stimuli were presented in the contralateral visual field [$t(7) = 4.475$, $P < 0.01$]. When TMS was delivered over IPS (Fig. 3c), there was no interaction between motion coherence and stimulus position [$F(1, 7) = 0.15$, $P = 0.71$], but the main effect of stimulus position was significant [$F(1, 7) = 7.91$, $P < 0.05$]. One-sample t tests showed that the cTBS effects in the contralateral visual field were significant for both 100 % coherent motion [$t(7) = 3.205$, $P < 0.05$] and 40 % coherent motion [$t(7) = 4.181$, $P < 0.01$], whereas there were no significant effects for the ipsilateral visual field. Stimulation of the vertex had no significant effect on motion direction discrimination (see Fig. 4). Note that since the vertex is located in the middle of the scalp, stimulus position in this condition was categorized as left versus right rather than contralateral versus ipsilateral visual field.

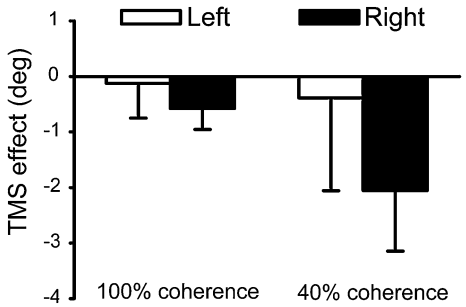

Fig. 4 TMS effects over the vertex on motion direction discrimination. Motion discrimination thresholds were measured for two coherence levels (100 or 40 %) at two locations (*left* and *right* visual fields). No significant TMS effect was found in all conditions. *Error bars* denote 1 SEM

Discussion

In this study, we report a double dissociation between the effects of cTBS delivered to V3A and MT+. V3A stimulation specifically impaired local motion processing, whereas MT+ stimulation specifically impaired global motion processing. Furthermore, IPS stimulation impaired motion discrimination at both coherence levels.

Among the visual regions involved in motion processing, V3A and MT+ are two pivotal areas (Newsome and Pare 1988; Salzman et al. 1990; Dupont et al. 1994; Tootell et al. 1995, 1997; Cornette et al. 1998; Sunaert et al. 1999; Braddick et al. 2001; Huk et al. 2001). Do these regions play different functional roles? If so, do they function in parallel with specialization for different aspects of motion processing, or is there a processing hierarchy with MT+ being the higher motion center? Most previous studies have found that V3A and MT+ exhibit similar functional properties when processing motion. Examples include the processing of motion speed (McKeefry et al. 2008), rotating and radial motion (Harvey et al. 2010), and first-order and second-order motion (Smith et al. 1998). However, in the present study, we discovered distinct roles for V3A and MT+ in local and global motion processing. Our results are consistent with evidence from human brain damage

studies: A patient who had a lesion in the left occipital lobe centered on visual areas V3 and V3A was specifically impaired in local but not global motion perception (Vaina et al. 2003, 2005). Furthermore, an fMRI study investigating the relationship between activation in motion-sensitive areas and motion coherence demonstrated a large difference in response profiles between MT+ and V3A (Rees et al. 2000). Responses in MT+ increased linearly with increasing motion coherence. On the other hand, responses in V3A were weak for motion coherence levels lower than 50 % and were strong for motion at 100 % coherence. Taken together, we suggest that while MT+ dominates in global motion processing, V3A plays an important role in local motion processing. This double dissociation implies that V3A and MT+ function at parallel stages rather than in a serial hierarchy.

In addition to the double dissociation between cTBS effects on V3A and MT+, we found that cTBS of IPS impaired direction discrimination for both global and local motion. This is consistent with previous reports of motion sensitivity within the human IPS (Sunaert et al. 1999). Motion sensitivity is particularly pronounced within areas IPS2 and IPS3 of the dorsal intraparietal sulcus medial (DIPSM) (Swisher et al. 2007; Wandell et al. 2007), which was targeted in the current study. Human IPS is also known as a critical area for visual decision making (see Heekeren et al. 2008 for a review; Tosoni et al. 2008; Ho et al. 2009; Kayser et al. 2010). As a putative homologue of monkey LIP (Sereno et al. 2001), this area may receive projections from V3A (Nakamura et al. 2001) and MT+ (Lewis and Van Essen 2000). Our findings support the idea that human IPS appears to be situated higher in the visual hierarchy and receives motion information from both V3A and MT+ to inform perceptual decision making. On the other hand, since the parietal cortex is also implicated in attentional modulation and spatial representation (Silver and Kastner 2009), the role of IPS in our motion direction discrimination task could be mediated via these high-level functions.

Transcranial magnetic stimulation is now an established investigative tool to selectively interfere neural processing. This interference has been known as a "virtual lesion" (Pascual-Leone et al. 2000). A number of flexible stimulation parameters, such as duration, frequency, intensity, and electric field orientation, have been found to alter the outcome of TMS application. cTBS, as a recently developed stimulation paradigm, is capable of producing consistent, long-lasting, powerful, and controllable electrophysiological and behavioral changes. The paradigm was initially tested and verified with human motor system (Huang et al. 2005). Recently, it has been applied in areas of cognition and perception. For example, cTBS over premotor cortex and superior temporal gyrus has been shown to reduce sensitivity to biological motion perception (van Kemenade et al. 2012b; Tarnutzer et al. 2013). Our study was the first to use cTBS to explore the roles of V3A and MT+ in global and local motion processing. The significant and reliable cTBS effects found in this study provide further strong evidence that cTBS is an efficient stimulation protocol not only for motor cortex but also for visual cortex. In the future, it would be important to take advantage of cTBS to investigate the causal contributions of cortical areas and networks in various cognitive functions.

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