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Brief communication

Repetitive TMS over posterior STS disrupts perception of biological motion

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Abstract

Biological motion perception, the recognition of human action depicted in sparse dot displays, is supported by a network of brain areas including the human posterior superior temporal sulcus (pSTS). We have used repetitive transcranial magnetic stimulation (rTMS) to temporarily disrupt cortical activity within the pSTS and subsequently measured sensitivity to biological motion. Sensitivity was measured for canonical (upright) point-light animations and for animations inverted 180 deg, a manipulation that renders biological motion more difficult to recognize. Observers were markedly less sensitive to upright biological motion following pSTS stimulation. In contrast, performance remained normal for inverted biological motion following pSTS stimulation, and normal for upright and inverted biological motion following stimulation over visual motion sensitive area MT+/V5. In connection with previous brain imaging results, our findings demonstrate that normal functioning of the posterior STS is required for intact perception of biological motion.

Keywords: Biological motion; Transcranial magnetic stimulation (TMS); Superior temporal sulcus (STS); Middle temporal area (MT/V5); Motion perception; Vision

1. Introduction

Viewing human movements, recognizing different actions, and interpreting body postures are visual tasks that we perform every day. Arguably, activities like these form the basis of many other, even more complex social behaviors, such as communication through signaling, deriving an individual's intentions, constructing our own actions in response, and even learning motor behaviors. We are so skilled at recognizing body movements, that humans can perform many of these tasks on the basis of kinematics alone, without the aid of color, form or shadows. Point-light biological motion, in which actions are depicted solely by the kinematics of light points placed on the joints of an actor, is an example of body perception stripped down to its most bare, and essential, components (Johansson, 1973).

Most individuals are quite adept at recognizing biological motion in point-light animations. Observers can accurately report gender (Cutting, 1978; Pollick, Lestou, Ryu, & Cho, 2002), identity (Cutting & Kozlowski, 1977; Hill & Johnston, 2001), affect (Dittrich, Troscianko, Lea, & Morgan, 1996; Pollick, Fidopiastis, & Braden, 2001), and even deceptive behavior from point-light animations (Runeson & Frykholm, 1981).

Some populations of individuals, however, have difficulty extracting the human form from the kinematics of the point-lights. Patients with lesions in posterior

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parietal cortex have difficulty discriminating biological from non-biological motion. The performance difficulties measured in these individuals exist despite normal performance on low-level motion tasks, such as coherence detection (Battelli, Cavanagh, & Thornton, 2003), and speed discrimination (Cowey & Vaina, 2000; Schenk & Zihl, 1997).

Recent neuroimaging studies highlight a critical role of posterior parietal cortex, in particular the posterior superior temporal sulcus (pSTS), as a neural locus for perception of bodies and body movements (Allison, Puce, & McCarthy, 2000). The pSTS has been found to be selectively activated when subjects view changes in eye gaze or mouth movements (Puce, Allison, Bentin, Gore, & McCarthy, 1998), body articulation (Beauchamp, Lee, Haxby, & Martin, 2002; Pelphrey et al., 2003), and point-light biological motion (Bonda, Petrides, Ostry, & Evans, 1996; Grossman & Blake, 2002; Howard et al., 1996; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001).

In this study, we evaluated whether an intact pSTS is necessary for the perception of biological motion in individuals with otherwise normal brain function. We have used low frequency 1 Hz repetitive transcranial magnetic stimulation (rTMS) to temporarily disrupt cortical functioning within two localized cortical regions. A survey of previous studies indicates the right hemisphere pSTS region to be more active than the left pSTS during biological motion perception (Bonda et al., 1996; Grossman et al., 2000; Pavlova, Lutzenberger, Sokolov, & Birbaumer, 2004; Pelphrey et al., 2003). A recent evoked potentials study by Hirai, Fukushima, and Hiraki (2003) demonstrated neural signals selective for biological motion over right, but not left, temporo-parietal cortex, corresponding to EEG coordinate T6. Thus the temporo-parietal region, specifically T6, is the brain site of experimental interest to this study. To control for more generalized effects of rTMS stimulation, performance was also tested following stimulation of a second brain site, left MT+/V5. Previous neuroimaging studies have demonstrated motion-sensitive MT+/V5 to be activated, but not preferentially, during perception of biological motion (Grossman et al., 2000). Additionally, restricting the stimulation of this control area to the opposite hemisphere as our experimental site of interest minimizes the possibility of cortical spread across stimulation sites as a result of the repetitive stimulation (e.g. Ferbert et al., 1992; Netz, Ziemann, & Homberg, 1995; Paus et al., 1997).

To test for a possible generalized effect of brain stimulation, observers were also asked to discriminate upside-down biological animations from upside-down scrambled motion. Like the inversion effect reported in face perception, inverted biological motion is much more difficult to recognize as biological (Pavlova & Sokolov, 2000; Sumi, 1984) despite being virtually identical (simply upside-down).

By having a two cortical stimulation sites and two psychophysical tasks, we were able to implement two different types of controls for our rTMS intervention (Robertson, Theoret, & Pascual-Leone, 2003). We predicted that rTMS to pSTS would disrupt upright, but not inverted biological motion (thus establishing the behavioral specificity of the effect). Furthermore, we predicted that rTMS to MT+/V5 would interfere with all motion tasks, but show no specificity for upright biological motion stimuli (thus establishing the topographic specificity of the pSTS effects). Non-specific distracting effects of rTMS, such as the physical sensation of the pulses, were further controlled using an off-line rTMS paradigm (Robertson et al., 2003).

2. Methods

2.1. Observers

Nine healthy individuals, aged 21–43 years (seven men, two women) with normal or corrected to normal vision participated in these experiments. Participants were checked for TMS exclusion criteria (Wassermann, 1998) and gave written informed consent as approved by the Harvard University and Beth Israel Deaconess Medical Center's Institutional Review Boards. The study was conducted in the Harvard-Thorndike General Clinical Research Center at BIDMC in order to provide the safest environment for the subjects.

2.2. Stimuli and procedure

Subjects were seated in a semidarkened room and viewed a 1 s point-light animation depicting various activities such as walking, kicking and throwing (Fig. 1). Animations were created by videotaping an actor with light points placed on the joints, digitizing the films and encoding the light points as x, y positions. Non-biological motion controls (''scrambled'' animations) were created by randomizing the starting position of each dot within a region approximating the biological figure. Unlike biological animations, which are instantly recognized as a human performing an action, scrambled animations appear as a meaningless cloud of dots with some overall flow in common. Inverted animations were created by flipping the biological and scrambled animations about the x-axis.

Animations were displayed on a Macintosh G3 laptop using Matlab (Mathworks, Inc.) in conjunction with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Target figures (biological, inverted or scrambled) averaged 3×8.5 deg of visual angle. Light points (.19 deg of visual angle) were displayed as black dots against a

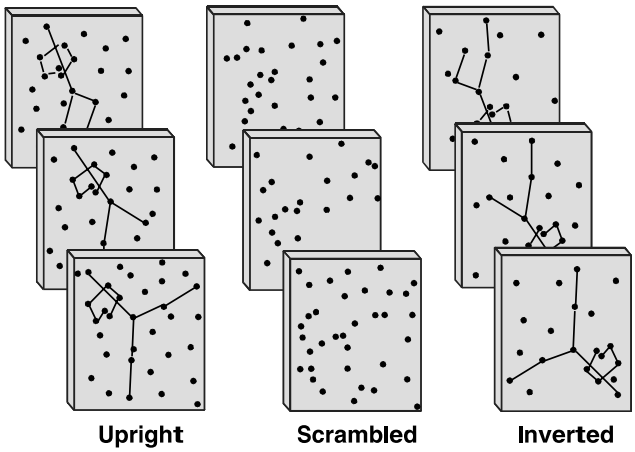

Fig. 1. Schematic of stimuli. Animations of point-light upright biological, scrambled, and inverted biological motion were embedded in noise arrays. Lines connecting dots in figure are for visualization only, and were not present in the experiment.

white background. The spatial location of the target figure was randomly jittered 1.4 deg from the display center on each trial to prevent tracking of a single dot. A fixation cross remained visible in the center of the display at all times.

The subjects' task in these experiments was to discriminate biological (upright or inverted) from scrambled motion. In normal viewing conditions, this is a trivially easy task, even for a naïve observer. Thus to guard against possible ceiling effects, the animations were embedded in a noise array generated from the same motions as the target sequence (i.e., a "walker" or "scrambled walker" was masked by scrambled walkers, "kickers" were masked by scrambled "kickers", etc.). Inverted biological motion is inherently more difficult to recognize as biological, thus rendering the discrimination task more difficult, and so these animations were embedded in fewer noise dots than in the upright condition.

Subject performance was calibrated individually prior to any brain stimulation. In a 2-1 staircase procedure, the number of noise dots required for threshold discrimination was determined. Subjects performed a two-alternative forced choice procedure (2AFC), indicating whether each trial depicted biological or scrambled motion. Subject responses were recorded by a keypress and subjects were not given accuracy feedback. The number of noise dots was increased after two correct responses, and decreased for each incorrect response, converging on the number of noise dots required for 71% accuracy. For each subject, the number of noise dots was fixed at this individually measured level for the remainder of the experiments. Thus, prior to any stimulation, performance in the upright and inverted conditions was fixed to be at threshold.

Following assessment of noise threshold a Pre-Stimulation Baseline sensitivity to the biological motion animations was measured. Subjects viewed 40 animations of each type (2×2 design—upright and inverted, biological and scrambled) embedded in the fixed level of noise and performed the same 2AFC as in the staircase procedure. Hits, misses, false alarms and correct rejections were recorded for each trial. Due to the different levels of noise required to mask the upright and inverted animations, these two trials types were presented in separate blocks, and subjects were informed as to the stimuli orientation.

TMS was then delivered using a MagStim stimulator (MagStim, Whitland, UK) and a commercially available 70 mm figure of eight Magstim stimulation coil. We applied a 10 min train of repetitive low-frequency (1 Hz) stimulation at 60% maximum stimulator output (equivalent to approximately 1.32 T) over one of the two brain sites, right pSTS or left MT+/V5. Previous studies have shown that 1 Hz stimulation temporarily reduces excitability of the cortex (within the stimulated area) and the excitability effects outlast the period of stimulation (Boroojerdi et al., 2000; Merabet et al., 2004; Mottaghy, Gangitano, Sparing, Krause, & Pascual-Leone, 2002). To aid in brain site localization, subjects wore a lycra swimmer's cap with a reference point positioned over the inion. Posterior STS was localized as T6 using the EEG 10/20 system (Hirai et al., 2003). MT+/V5 was localized by the induction of moving visual phosphenes with single-pulse stimulation (Stewart, Battelli, Walsh, & Cowey, 1999). For this localization, we stimulated a 3×3 grid of 9 points spaced 1 cm apart and centered 3 cm dorsal, 5 cm lateral to the inion, approximately over area MT+/V5. Participants were blindfolded and instructed to keep their eyes closed. Single pulse TMS was delivered at intensities ranging from 30 to 90% of maximum stimulator output or until the participant reported seeing phosphenes (Battelli, Black, & Wray, 2002; Beckers & Zeki, 1995). Eight subjects reported seeing moving phosphenes during single-pulse stimulation, allowing more precise localization of MT+/V5. The moving phosphenes were always experienced at stimulator outputs greater than that used during the repetitive stimulation (a minimum of 70% stimulation output required to elicit phosphenes, 60% stimulator output used during rTMS).

Immediately following the repetitive stimulation over the targeted brain site, subjects performed the biological motion sensitivity task (same task as the Pre-Stimulation Baseline). The time required to perform the psychophysical task (approximately 8 min) is within that for which 10 min trains of slow frequency rTMS have been shown to have lasting effects in parietal regions (Hilgetag, Burns, O'Neill, Scannell, & Young, 2000). After completion of the task, observers rested for 15 min to allow complete recovery from the stimulation. Stimulation was then applied to the remaining brain site in the opposite hemisphere, and the subject again performed the

task. The order of brain site stimulation was counterbalanced across observers, which allowed us to control for any effects of "double-dose" of stimulation (there were none).

Following the second stimulation, task completion and a 15 min recovery period, participants repeated the task to obtain a final Post-Stimulation Baseline. Psychophysical data were analyzed using a mixed effects repeated measures analysis of variance.

3. Results

3.1. Psychophysical results

Individuals ranged greatly in their ability to tolerate added noise to the displays while still performing the discrimination task. However, all subjects tolerated much less noise in the inverted discrimination task than in the upright discrimination task. The number of noise dots tolerated in the upright condition averaged 111.1 dots (SD 44.6 dots). Noise levels for the inverted condition averaged 42.8 dots (SD 26.4), almost one-third the level of noise tolerated in the upright condition.

Prior to any stimulation subjects were able to easily discriminate the two types of animations (Fig. 2). The average sensitivity score for the upright biological animations was 1.51 d-prime (d′) units, and sensitivity for the inverted was 1.46 d′ units. This is not surprising given that task difficulty was set based on discrimination thresholds measured just prior to this sensitivity task.

A mixed effects analysis of variance revealed a main effect of stimulation site on sensitivity ($F = 11.57$; $p < .01$). Post-hoc comparisons among the different conditions (Tukey HSD) revealed stimulation over pSTS resulted in significantly worsened discrimination performance in the upright biological motion condition ($p < .01$). Sensitivity scores for upright biological motion dropped on average to 1.12 d′ units following rTMS as compared with baseline. In contrast, sensitivity to the inverted biological motion remained unchanged from baseline, at 1.41 d′ units ($p > .05$). Stimulation over MT+/V5 did not change performance on either the upright or inverted biological motion discriminations (upright mean 1.53; inverted mean 1.61; both $p > .05$).

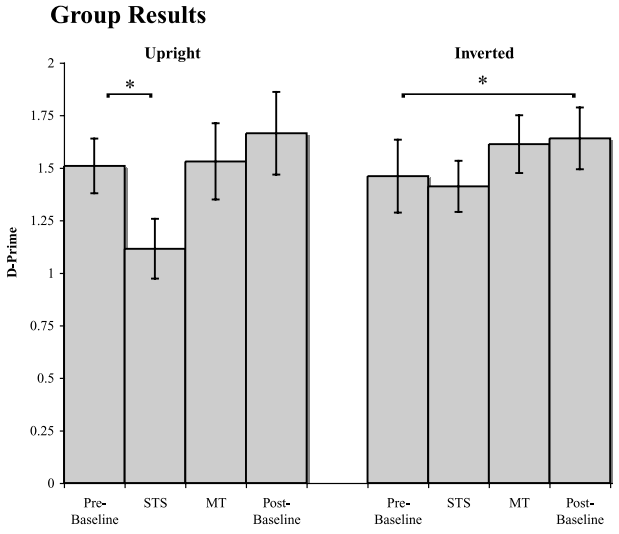

Fig. 2. Group psychophysical results. Upright biological motion and inverted biological motion sensitivity before and after rTMS stimulation. Asterisk (*) indicates a significant difference in sensitivity scores from Baseline ($p < .05$). Error bars indicate 1 standard error.

A Post-Stimulation Baseline measure indicated that observers fully recovered from the effects of stimulation within 15 min. Post-hoc comparisons indicate no difference in Pre- and Post-Baseline performance in the upright condition ($p > .05$). Post-Baseline performance in the inverted condition was significantly improved from the Pre-Baseline ($p < .05$), suggesting subjects may have been able to learn through repeated task performance.

3.2. Stimulation site reconstruction

High resolution anatomical images in conjunction with frameless stereotaxy (BrainSight™, Rogue Research, Montreal, Canada) were used to visualize the projected cortical target of the T6 and MT+/V5 stimulation sites in two subjects (Fig. 3). The projected target of stimulation over T6 (presumed to be STS) corresponded to the posterior extent of the superior temporal sulcus, the same region implicated in biological motion responsive in EEG and fMRI studies (Beauchamp, Lee, Haxby, & Martin, 2003; Bonda et al., 1996; Grossman et al., 2000; Hirai et al., 2003; Vaina, Belliveau, des Roziers, & Zeffiro, 1998). The MT+/V5 stimulation site projected onto the ascending extent of the lateral occipital sulcus, corresponding to reported location of human MT+/V5 as determined through neuroimaging (Huk, Dougherty, & Heeger, 2002; Sunaert, Van Hecke, Marchal, & Orban, 1999; Tootell et al., 1995; Watson, 1996; Watson et al., 1993) .

4. Discussion

These experiments found that low frequency rTMS over the posterior extent of the human STS temporarily impairs perception of biological motion. Stimulation over MT+/V5 did not affect observers' ability to detect and discriminate the biological animations in the noise arrays. These findings are the first to demonstrate that pSTS is critical for the perception of biological motion.

These results are in agreement with the neuropsychological literature, which has shown that individuals with lesions covering posterior parietal cortex have poor sensitivity to biological motion despite intact low-level

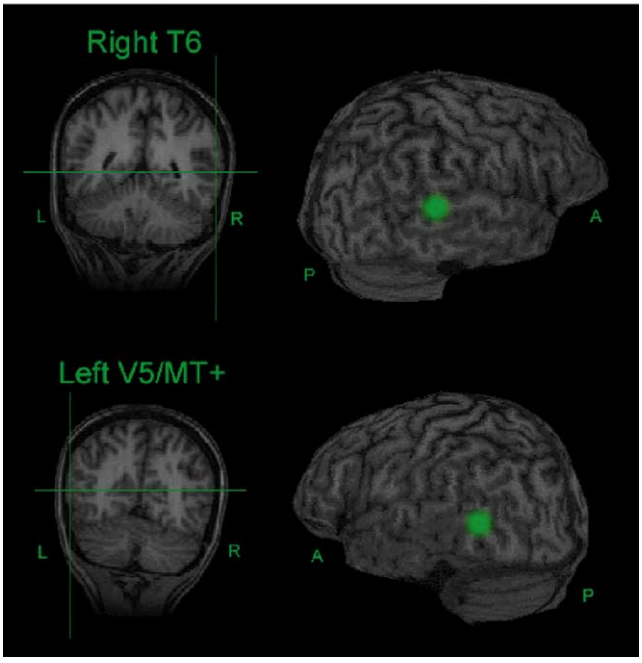

Fig. 3. Coronal and whole-brain visualization of stimulation sites. Two participants (author EG shown) provided high resolution anatomical MRI images which were co-registered with the stimulation device. Cross-hairs on coronal image indicate focus of the projected stimulation path as shown on the whole-brain image.

motion perception (Schenk & Zihl, 1997). It has been suggested that the difficulties experienced by these individuals are due to damaged attention mechanisms required to perform high-level motion tasks (Battelli et al., 2001). Indeed, biological motion perception, which has often been described as effortless, seems to depend on a functioning attentional system (Battelli et al., 2003; Thornton, Rensink, & Shiffrar, 2002). It is also interesting to note that in our study, rTMS over pSTS did not affect sensitivity to the inverted biological motion. Recognizing inverted biological motion presumably requires attention in the same way that recognizing upright biological motion does, and thus is it unlikely that the deficits in sensitivity we measured following stimulation are a result of dampening the attentional system as a whole. It is also noteworthy that a previous neuroimaging study has shown BOLD response to inverted biological motion to be approximately half that of canonical (upright) biological motion (Grossman & Blake, 2001). The implication on the current study is that that the impact of stimulation over pSTS may be weakened for perception of inverted biological motion. It is also possible, that because subjects were able to complete the discrimination task with some degree of accuracy, additional neural machinery is recruited during recognition of the inverted animations, machinery that is not impaired by stimulation over the parietal and extrastriate brain sites.

One of the surprising findings from this study was that observer performance was unaffected by stimulation over MT+/V5. This extrastriate region was chosen as a stimulation site because of its motion-selectivity, a functional characteristic that makes MT+/V5 a brain area that likely feeds forward into the more anterior pSTS. Psychophysical studies have shown that spatio-temporal integration of the light points is required to recognize point-light animations as biological (Ahlström, Blake, & Ahlström, 1997), a computation believed to be accomplished by MT+/V5. Indeed, neuroimaging studies have found MT+/V5 to be activated during perception of point-light biological motion, although not preferentially (Grossman et al., 2000). Additionally, previous stimulation studies have shown motion discrimination to decline following single-pulse stimulation over MT+/V5 (Ellison, Battelli, Cowey, & Walsh, 2003). Previous stimulation studies have also shown, however, that the effects of brain stimulation over MT+/V5 are varied depending on low-level stimulus properties and cognitive demands of the task (Matthews, Luber, Qian, & Lisanby, 2001; Walsh, Ellison, Battelli, & Cowey, 1998), and may not be reflected so much in detection sensitivity as decision bias (Hotson & Anand, 1999). Indeed, the purpose of measuring hits and false alarm responses in our tasks was to measure if changes in biases occurred as a result of stimulation (none were found). Thus, we are left to conclude that if stimulation over MT+/V5 affected the low-level motion signals in our subjects in such a way as to alter the perception of our stimuli, our behavioral measures were not sufficiently sensitive to measure these changes (despite being sensitive enough to measure impaired biological motion sensitivity following stimulation over pSTS). It is also important to note that some authors have argued that biological motion perception is possible without any motion cues at all and is instead driven by configural, or shape, information (Beintema & Lappe, 2002). The results from this study would support such a hypothesis.

One might argue that although repetitive stimulation was applied over one brain site, the contralateral "intact" brain area (left pSTS or right MT+/V5) could be responsible for the relatively good performance in these tasks. In all likelihood, some effects of the repeated stimulation on homologous brain areas in the opposite hemisphere occurred via spread through transcallosal connections (Hilgetag et al., 2000; Paus et al., 1997). To fully control for the possible effects of an intact hemisphere one must simultaneously stimulate both hemispheres. Because we did not apply bilateral stimulation, it is possible that the relatively good performance was due to normal cortical processing in the intact hemisphere. However, this hypothesis would actually predict the opposite patterns of results than we found. Human MT+/V5 receives input corresponding to a contralateral visual field representation (Huk et al., 2002), while the cortical organization of pSTS is thought to include the

full visual field (Grossman et al., 2000). Thus, for our tasks in which stimuli were presented foveally, the single "intact" MT+/V5 would only receive half the stimulus (the half visible in the opposite visual field), while pSTS would have full access to the visual input. The prediction would then be that performance should be worse following stimulation over MT+/V5 than by pSTS because only half the information is being processed normally as opposed to the entire visual field, the opposite pattern of results than we found. This effect would be further magnified in trials for which the slight spatial jitter applied to the target moved the stimulus further away from the "intact" visual field for MT+/V5 stimulation. Thus we argue that relatively good performance following brain activation is not a reflection of remaining intact function in the contralateral hemisphere, but reflects some residual function within the stimulated brain area. Differential effects of stimulation reflect specialization of the pSTS for the task demands of our biological motion discrimination task.

Biological motion perception has been suggested to be one stage of a cortical network for social perception (Adolphs, 2001). In this model, the human superior temporal sulcus (STS) is reciprocally connected to the orbito-frontal cortex and amygdala, and provides the cues necessary for recognition of social, biological events such as recognition of emotional expression and personal intention. Psychophysical evidence supports the link between low-level perception and social behavior, including evidence of impaired biological motion perception in individuals with autism, a population with profound social difficulties (Blake, Turner, Smoski, Pozdol, & Stone, 2003), and above average biological motion perception in those individuals with William's syndrome, a disorder associated with highly social behavior (Jordan, Reiss, Hoffman, & Landau, 2002). It has also been proposed that body perception (and biological motion perception) are closely related to motor learning and action planning, tasks involving premotor cortex, among other brain areas (Buccino et al., 2001; Decety & Grezes, 1999). It remains to be seen the full range of cognitive and motor processes which are affected by disrupting cortical processing within the STS, and the effects of brain stimulation over other brain sites on biological motion sensitivity. The present study provides a functional marker of STS disruption by rTMS that might be useful for future studies evaluating the role of STS in higher forms of social perception and cognition.

Acknowledgments

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