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Discoveries in Cognitive Science

an open access journal

A Causal Role of the Right Superior Temporal Sulcus in Emotion Recognition From Biological Motion

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Keywords: biological motion, superior temporal sulcus, emotion recognition, transcranial magnetic stimulation

ABSTRACT

Understanding the emotions of others through nonverbal cues is critical for successful social interactions. The right posterior superior temporal sulcus (pSTS) is one brain region thought to be key in the recognition of the mental states of others based on body language and facial expression. In the present study, we temporarily disrupted functional activity of the right pSTS by using continuous, theta-burst transcranial magnetic stimulation (cTBS) to test the hypothesis that the right pSTS plays a causal role in emotion recognition from body movements. Participants ($N = 23$) received cTBS to the right pSTS, which was individually localized using fMRI, and a vertex control site. Before and after cTBS, we tested participants' ability to identify emotions from point-light displays (PLDs) of biological motion stimuli and a nonbiological global motion identification task. Results revealed that accurate identification of emotional states from biological motion was reduced following cTBS to the right pSTS, but accuracy was not impaired following vertex stimulation. Accuracy on the global motion task was unaffected by cTBS to either site. These results support the causal role of the right pSTS in decoding information about others' emotional state from their body movements and gestures.

INTRODUCTION

The dynamics and kinematics of body movements play a vital role in the expression and perception of emotion and other social cues. Indeed, the ability to detect, identify, and respond appropriately to these dynamic nonverbal cues is central to social competence (Mehrabian & Ferris, 1967; Rosenthal, Hall, DiMatteo, Rogers, & Archer, 1979). Neuroimaging evidence has long implicated the right posterior superior temporal sulcus (pSTS) as a cortical region central to the perception of social cues from body movements (Bonda, Ostry, & Evans, 1996; Grossman & Blake, 2002; Puce, Allison, Bentin, Gore, & McCarthy, 1998). This region shows a preference for dynamic bodies and faces over static, and it is sensitive to the configuration of a moving body (Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011; Thompson, Clarke, Stewart, & Puce, 2005). While evidence indicates that both the left pSTS (Saygin et al., 2007; van Kemenade, Muggleton, Walsh, & Saygin, 2012) and right pSTS are involved in the perception of body movement, there is evidence for the response to body motion to be more consistent in the right hemisphere (Bonda et al., 1996; Engell & McCarthy, 2013; Grossman & Blake 2002; Pavlova, Lutzenberger, Sokolov, & Birbaumer, 2004; Pelphrey, Morris, &

Citation: Basil, R. A., Westwater, M. L., Wiener, M., & Thompson, J. C. (2017). A Causal Role of the Right Superior Temporal Sulcus in Emotion Recognition From Biological Motion. *Open Mind: Discoveries in Cognitive Science, 2*(1), 26–36. https://doi.org/10.1162/opmi_a_00015

DOI: https://doi.org/10.1162/opmi_a_00015

Received: 11 November 2016
Accepted: 6 September 2017

Competing Interests: The authors declare no competing financial interests.

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McCarthy 2004; Pitcher, Duchaine, & Walsh, 2014; Puce et al., 1998). Greater functional magnetic resonance imaging (fMRI) response selectivity to point-light displays (PLDs) of biological motion in the right pSTS is also associated with larger, more complex social networks, implying that the coding of the movements of others in this region is important for social abilities (Dziura & Thompson, 2014). However, common neuroimaging techniques, such as cross-sectional fMRI, are correlational and therefore limited in their ability to establish the causal role of a brain region in a perceptual or cognitive function. Here, we used fMRI-guided continuous, theta-burst transcranial magnetic stimulation (cTBS), a specific repetitive transcranial magnetic stimulation (rTMS) protocol, to examine whether the right pSTS is causally involved in the perception of emotional states conveyed by body movements.

Understanding the causal role of the right pSTS in the perception of dynamic social stimuli is important, as impaired processing of face and body stimuli in this region has been linked to social deficits in autism spectrum disorder (ASD; Alaerts et al., 2014; Koldewyn, Whitney, & Rivera, 2011; Pavlova, 2012) and schizophrenia (Kim, Doop, Blake, & Park, 2005; Kim, Norton, McBain, Ongur, & Chen, 2013). More recently, decreased fMRI activity to point-light biological motion stimuli in the right pSTS has been proposed as a "neurobiomarker" for ASD (Björnsdotter, Wang, Pelphrey, & Kaiser, 2016). Studies of brain structure also point to altered cortical thickness of the pSTS in neurodevelopmental disorders (Zilbovicius et al., 2006), and protracted maturation of this region has been associated with altered functional network differentiation in children and adolescents with ASD (Shih et al., 2011). Shih et al. (2011) postulate that atypical development of the pSTS could indicate impaired functional specificity of this region in individuals with ASD, and this might contribute to the inability of some with neurodevelopmental disorders to discriminate dynamic social cues, such as subtle shifts in body language, that convey the intentions or emotions of another. As such, increased understanding of the role of the right pSTS in the perception and discrimination of social information from biological motion is important for future work with these clinical populations.

Several studies have investigated biological motion perception using offline repetitive transcranial magnetic stimulation (rTMS) to the pSTS, where "offline" indicates that stimulation does not occur simultaneously with the task. Accordingly, "online" stimulation protocols administer stimulation concurrently with the task itself, such that stimulation occurs at a predetermined point in time during the task protocol, typically with either a single pulse of TMS, or a brief, high-frequency burst of stimulation. Online stimulation protocols are preferred when the causal role of a brain region has been well established and the precise timing of a region is under investigation. Offline stimulation protocols are useful when the goal is to first establish the causal involvement of a brain region in a specific cognitive function. Grossman, Battelli, and Pascual-Leone (2005) previously reported that 1 Hz repetitive TMS (rTMS) to the right pSTS impaired discrimination of upright point-light biological motion when presented in noise. Similarly, Vangeneugden et al. (2014) used 1 Hz rTMS to show that the right pSTS was involved in discriminating walking direction from biological motion. One study (van Kemenade et al., 2012) used cTBS to examine the role of left pSTS in biological motion discrimination from noise, finding a nonsignificant trend for reduced detection of biological motion from noise.

Potential advantages of cTBS include similar effect sizes to online stimulation, significantly shorter stimulation periods (<1 min), and longer duration of effect (60–90 min) compared to 1 Hz rTMS (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005; Thut & Pascual-Leone, 2010). Given prior work, we sought to determine if pSTS function extends further to the coding and identification of actions conveying emotional information. We examined the effects of disruption by continuous theta-burst rTMS (cTBS) on a point-light emotion discrimination task (Atkinson, Dittrich, Gemmell, & Young, 2004). We chose this task because the

discrimination of emotions from gestures and body movements represents a key social ability. To exclude the possibility that any observed effects of cTBS were due to an effect on the more general global motion discrimination process, we compared subjects' performance on the emotion discrimination task to a nonbiological motion control task. Furthermore, we used fMRI-guided neuronavigation of the TMS coil to account for individual differences in the precise location of the right pSTS region involved in processing biological motion. It was hypothesized that cTBS targeted over the right pSTS would significantly impair both accuracy and reaction time to the emotion recognition task, relative to stimulation of a vertex control site. We did not anticipate cTBS to the right pSTS or vertex to impair performance on the global motion control task.

MATERIALS AND METHOD

Participants

Twenty-three healthy, right-handed adults (13 female; M_{age} = 25.2 y; SD = 3.8) with normal or corrected-to-normal vision participated in the study. Exclusion criteria for both the fMRI and TMS sessions were history of traumatic brain injury, diagnosis of a neurological disorder, ferromagnetic implants, or current use of psychotropic medication. Prior to participation, participants provided written informed consent and completed both MRI and cTBS safety screening procedures. The study procedure and all relevant materials were approved by the George Mason University Human Subjects Review Board (HSRB). Participants were informed at each session that they were free to withdraw from the study at any time for any reason, and they received monetary compensation for their time.

fMRI Localizer: Identification of Right pSTS Target Site

fMRI Data Acquisition and Preprocessing To ensure accurate targeting of right pSTS for the cTBS, we first collected blood oxygen-level dependent (BOLD) fMRI data as participants viewed a block design paradigm, consisting of five blocks of scrambled and intact 12-dot PLDs (Dziura & Thompson, 2014). Intact PLDs performed different actions, such as running, skipping, and jumping. Scrambled figures had the same trajectories as the intact PLDs, but their starting positions were random. All stimuli were obtained from the Carnegie Mellon University Graphics Lab Motion Capture Database (http://mocap.cs.cmu.edu). The 2-s videos were presented during data acquisition in blocks of 16 s per condition, alternating with a 12-s fixation block, using Neurobehavioral Systems Presentation software (Version 16.3). To ensure active viewing of the stimuli, participants were instructed to press a button with their right index finger upon seeing a stimulus repeat (1-back). Visual stimuli were presented on a rear projection screen that was viewed using a head coil-mounted mirror.

BOLD images were acquired on a 3T Siemens Allegra Magnetom using a one-channel quadrature birdcage head coil. Parameters for these functional runs were the following: 172 gradient echo echoplanar images, 33 interleaved axial slices, 3 mm slice thickness (1 mm gap), repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle = 70°, matrix size = 64 × 64 mm, field of view (FOV) = 192 mm^2. Upon completion of the task, a T1-weighted, whole-head structural scan was acquired using a three-dimensional, magnetization-prepared, rapid-acquisition gradient echo (MPRAGE) pulse sequence. The following parameters were used for these scans: 160, 1-mm slices with sagittal acquisition, TR = 2300 ms, TE = 3.37 ms, flip angle = 7°, matrix size = 256 × 256 mm, FOV = 1260 mm^2.

Functional data were analyzed using the fMRI Expert Analysis Tool (FEAT) within the FSL software package (version 6.0; http://fsl.fmrib.ox.ac.uk). Preprocessing involved correction for signal inhomogeneity, brain extraction, motion correction, linear registration to the T1-weighted anatomical images, and spatial smoothing at 6 mm FWHM. Intact motion and scrambled motion blocks, as well as head motion regressors, were entered into a linear regression at each voxel, using generalized least squares (GLS) with a voxel-wise, temporally and spatially regularized autocorrelation model. A Gaussian-weighted running line smoother (100s FWHM) was also included in the model to account for drift. Individual subject regions of interest (ROIs) were created from peak voxels in the right pSTS exhibiting activation in the intact vs scrambled PLDs at $p < .05$ (uncorrected). For subject-specific localization of the right pSTS, ROIs were created in each subject's native space. The average MNI (Montreal Neurological Institute) coordinates for the right pSTS was 56.57 (4.90), −43.48 (5.76), 12.87 (9.81). The spatial distribution of individually derived pSTS ROIs is presented in Figure 1A. Individual Z-statistic maps from three representative subjects are shown in Figure 1B.

Theta Burst Stimulation of the Right pSTS & Vertex

Apparatus and Stimuli Continuous TBS of a three-pulse burst at 50 Hz, with a 5 Hz inter-burst-interval was delivered in an uninterrupted train of 600 pulses, over each participant's functionally localized right pSTS and vertex (as used by Pitcher, Garrido, Walsh, & Duchaine, 2008, the midway point between the nasion and the inion, equidistant from the left and right intertragal notches). Continuous TBS was delivered at 40% of maximal stimulator output (Huang et al., 2005) by a Magstim Super Rapid+ Magnetic Stimulator with a 70 mm diameter figure-of-eight, air-cooled coil (Magstim, United Kingdom), in conjunction with Brainsight Image Analysis and Neuronavigation Software (Version 2.3; 2016). This intensity was derived from

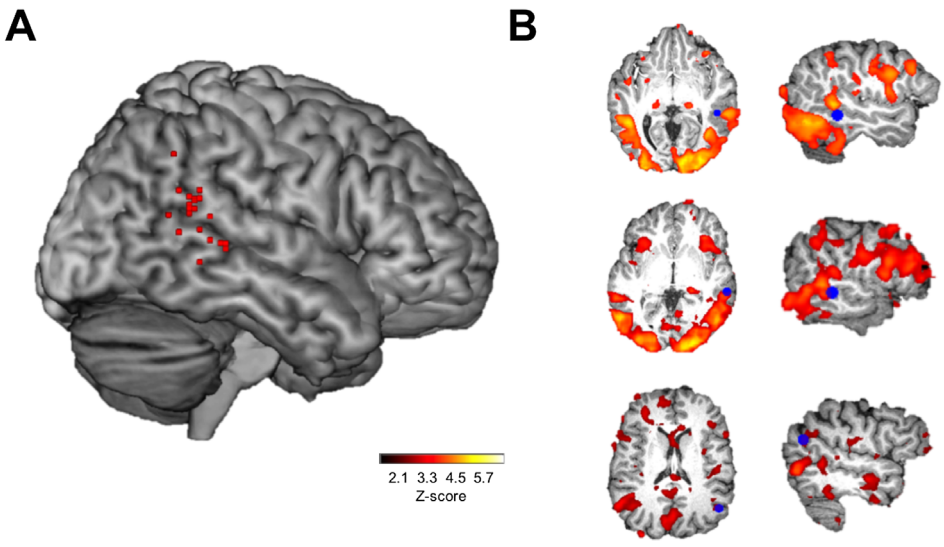

Figure 1. Single-subject fMRI activation maps and cTBS stimulation sites. The right posterior superior temporal sulcus (pSTS) continuous, theta-burst transcranial magnetic stimulation (cTBS) site for each subject was determined from an fMRI localizer, comprised of intact and scrambled biological motion stimuli. Stimuli were presented as point light displays (PLDs). Stimulation site was determined from peak voxel activation in the right pSTS for intact > scrambled contrast. (A) Subjects ($N = 23$) cTBS stimulation sites overlaid on the MNI-152 template brain. (B) Uncorrected Z-statistic maps of intact > scrambled contrast for three representative subjects. Activation maps were thresholded for visualization, and regions of interest (ROI) were overlaid.

previous studies (Borckardt et al., 2008). Participants were provided hearing protection for both stimulation sessions.

Procedure

In a randomized and counterbalanced design, participants were presented with dynamic stimuli of PLDs, which comprised the biological stimuli, as well as global nonbiological motion stimuli in different directions in separate alternating blocks (see Figure 2C). Stimuli were presented on a Dell E1911 19″ Monitor with 1440 × 900 resolution and a refresh rate of 60 Hz, using Neurobehavioral Systems Presentation Software (Version 17.2; 2015). Each stimulus was presented for 1,200 ms, and each block contained 48 trials (16 trials per condition). Each block was 3 min in duration.

On each trial, participants completed a three-alternative forced choice task, where they were instructed to choose the emotion (in the case of biological motion) or the type of motion (in the nonbiological motion trials) as quickly and accurately as possible. For the biological motion task, PLDs performed actions to convey one of the three emotions (Figure 2A). There were 10 actions for each of the three emotions, and stimuli came from a set of full-body 13-dot PLDs created by and validated by Atkinson and colleagues (2004). The stimulus set included, among others, shaking of the fist or arms (angry), a vertical jump or skipping (happy), and

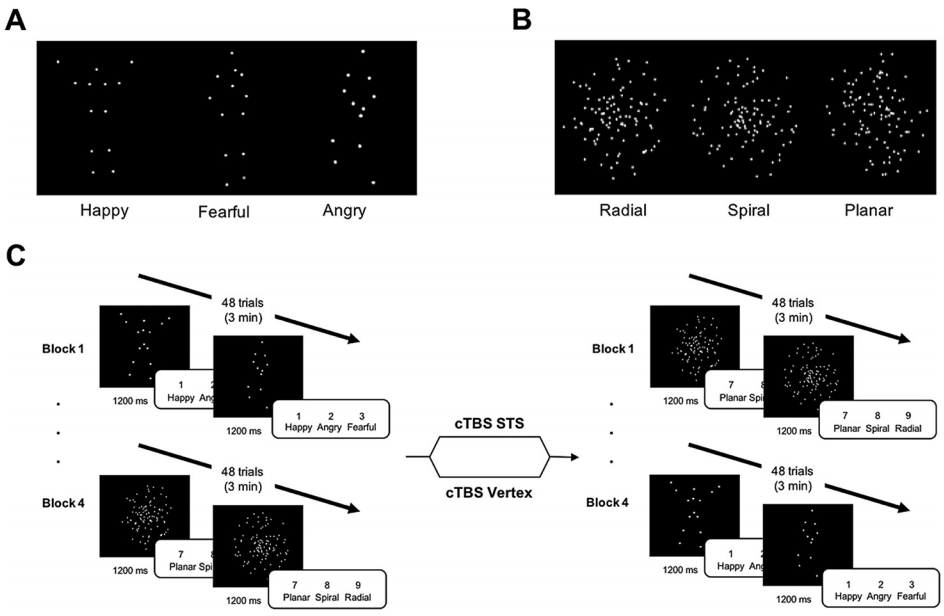

Figure 2. Biological and nonbiological motion stimuli and task paradigm. (A) Biological stimuli were PLDs (point-light displays) that conveyed three emotions: happy, fearful, and angry. (B) Nonbiological motion stimuli consisted of dots moving with the same pattern in three conditions: radial, spiral, and planar. Radial motion was defined as dots moving with the same rho but separate theta values. Dots for spiral motion had the same theta but separate rho values. Dots had the same rho and theta for planar motion. Each condition had 10 actions. (C) Participants completed four randomized task blocks (two biological motion; two nonbiological motion) prior to cTBS (continuous, theta-burst transcranial magnetic stimulation) to either the right pSTS (posterior superior temporal sulcus) or vertex. Four more randomized task blocks (two biological motion; two nonbiological motion) were completed after cTBS. Each block was 3 min. Each participant completed the paradigm twice for cTBS of the pSTS and vertex. Stimulation site was counterbalanced across participants.

cowering or turning from camera (fearful). The global motion task required subjects to view a series of dots and choose whether the motion of the dots appeared to be unidirectional (i.e., planar), radiating from a center point (radial), or circulating around a center point (spiral; see Figure 2B). Stimuli for the global motion control task were created in MATLAB (v.R2012a). Stimuli consisted of 100 white dots (0.2°) on a black background. Dots moved at a speed of 2°/sec, with a lifetime of 7 frames, within a circular aperture of 12°. Noise dots (60%) moved in a random direction for the duration of their lifetime. Coherent dots (radial, rotational, or planar) moved with the same pattern, with the pattern first determined in polar coordinates and converted to Cartesian coordinates for drawing each frame. Coherent radial motion (expansion/contraction) was determined by making all dots move with the same rho (Spearman's rank-ordered correlation coefficient) but with each dot having a separate theta. Coherent spiral motion (clockwise/counterclockwise) was created by making all dots move with the same theta and separate rho. Planar motion (left or right) was created by making dots move with the same theta and rho. As in the biological motion task, there were ten actions per condition. Participants were seated 75 cm in front of a desktop screen when completing the biological and nonbiological motion tasks. Each participant remained seated for cTBS stimulation. The visual angle of the stimuli was 9.4°, and it remained the same for all conditions. Subjects were asked to respond using designated response keys on a keyboard. Numeric keys 1, 2, and 3 corresponded with biological motion stimuli, and keys 6, 7, and 8 were used for nonbiological motion trials.

Before the experiment began, participants completed a training session to familiarize themselves with both the stimuli and the button coding. In total, subjects completed four blocks of biological motion (two pre-cTBS, two post-cTBS) and four blocks of nonbiological motion (two pre-cTBS, two post-cTBS) in a counterbalanced fashion. Continuous TBS was performed upon completion of the first four blocks (see Figure 2C). Subjects remained seated while the experimenter and an assistant located the stimulation site (i.e., vertex, pSTS), positioned the coil, and applied stimulation. Following cTBS, subjects were repositioned, facing the computer screen, and instructed to complete the remaining task blocks. Each session lasted approximately 40 min in total.

RESULTS

The cTBS manipulation aimed to temporarily disrupt participants' ability to identify emotional states from biological motion stimuli following cTBS over the right pSTS. As an active control, the vertex was stimulated. We did not anticipate a decrease in subjects' ability to label emotional states after cTBS to the vertex. A paired samples t test indicated nonsignificant differences between accurate identification of biological ($M = 0.86$, $SD = 0.07$) and nonbiological ($M = 0.88$, $SD = 0.16$) stimuli before cTBS, $t(22) = 0.928$, $p = .329$. As such, any observed differences in accuracy across the task conditions were hypothesized to reflect cTBS stimulation, not task difficulty. Statistical analyses of task session data were completed in IBM SPSS Statistics (v.19). We conducted two, two-by-two repeated measures ANOVAs to examine the effect of cTBS site (right pSTS and vertex) and stimulus type (biological or nonbiological) on accuracy and reaction time (RT). Mean accuracy and RT values for each condition are shown in Table 1.

The two-by-two repeated measures ANOVA of accuracy showed a significant main effect of cTBS site, $F(1, 22) = 10.87$, $p = .003$. A main effect of stimulus type also reached statistical significance, $F(1, 22) = 8.50$, $p = .008$. Analyses further indicated a significant

Table 1. Accuracy and reaction time values for biological and nonbiological motion conditions pre- and post-cTBS.

	pSTS		Vertex	
Accuracy	Pre-cTBS	Post-cTBS	Pre-cTBS	Post-cTBS
Biological	88 ± 6%	84 ± 9%	84 ± 7%	87 ± 8%
Nonbiological	90 ± 10%	93 ± 9%	86 ± 20%	90 ± 15%
Reaction time				
Biological	1,262 ± 280 ms	1,137 ± 226 ms	1,308 ± 259 ms	1,203 ± 202 ms
Nonbiological	1,146 ± 286 ms	980 ± 222 ms	1,158 ± 297 ms	1,014 ± 184 ms

Notes: Accuracy (% correct) and reaction time (ms) values are presented as $M \pm SD$. cTBS = continuous, theta-burst transcranial magnetic stimulation; pSTS = posterior superior temporal sulcus.

two-way interaction of cTBS site and stimulus type, $F(1, 22) = 4.93$, $p = .037$. These effects are shown in Figure 3. Post-hoc paired samples t tests revealed that the change in accuracy when cTBS was targeted over the right pSTS significantly differed between the two stimulus types, $t(22) = -4.60$, $p < .001$. Post-hoc comparisons further demonstrated that participants' ability to accurately identify emotions from biological motion was significantly impaired following cTBS to the right pSTS but not to the vertex, $t(22) = -5.77$, $p < .001$. Additional post-hoc

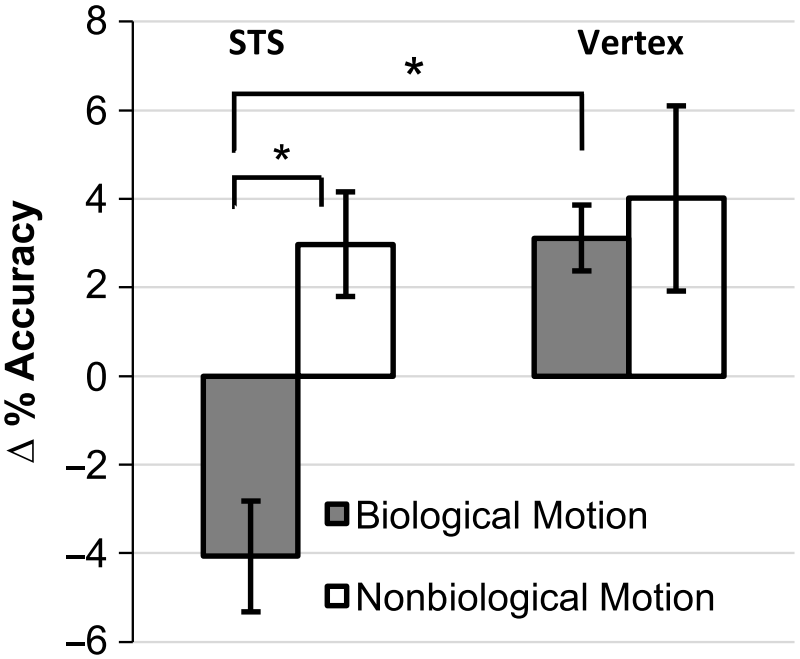

Figure 3. Mean differences in percentage accuracy change by stimulus condition (biological motion and nonbiological motion) cTBS site. Continuous transcranial magnetic stimulation (TBS) over right posterior superior temporal sulcus (pSTS) impaired emotional recognition through biological motion, but not nonbiological motion. The y axis denotes mean change in accuracy (% correct) from pre- to post-cTBS (continuous, theta-burst transcranial magnetic stimulation), where a value of 0 would indicate no change. An asterisk denotes a significant ($p < .001$) difference. Error bars indicate SEM.

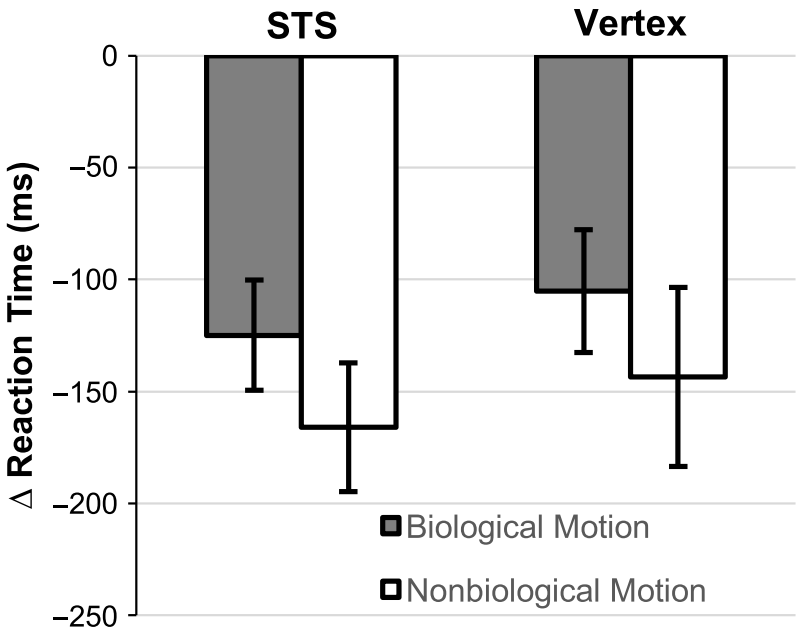

Figure 4. Mean differences in change in reaction time by condition (biological and nonbiological motion) by cTBS site. Reaction time (RT; ms) to either stimulus type was not significantly changed following continuous, theta-burst transcranial magnetic stimulation (cTBS) to the right posterior superior temporal sulcus (pSTS) and vertex. The *y* axis denotes a change in RT from pre- to post-cTBS, where more negative values indicate greater decreases in RT (i.e., faster responding) from pre- to post-cTBS. Error bars indicate SEM.

comparisons indicated that accurate discrimination of nonbiological motion stimuli did not differ significantly by cTBS site, $t(22) = -0.45$, $p = .66$.

A two-by-two repeated measures ANOVA of RT did not demonstrate a main effect of cTBS site, $F(1, 22) = 0.37$, $p = .547$, or stimulus type, $F(1, 22) = 2.89$, $p = .103$. The two-way interaction of cTBS site and stimulus type was also nonsignificant, $F(1, 22) = 0.00$, $p = .984$. These findings are illustrated in Figure 4.

DISCUSSION

The present study found that disruption of the right pSTS using cTBS leads to selective impairment in the recognition of emotions conveyed by human movements. We used fMRI to target a right pSTS region in each participant, as this region has been previously implicated in the visual processing of biological motion and in "social networks" of the brain. We found that right pSTS-targeted cTBS reduced the accuracy of the identification of different emotional point-light stimuli. The detrimental effects of cTBS to this region did not extend to the recognition of nonbiological motion, as we found no significant impairment in the identification of different global motion stimuli. The effect of cTBS to the right pSTS was limited to recognition accuracy; RT was not significantly changed by cTBS. This absence of an RT effect is not unprecedented, as similar findings were reported by both Grossman et al. (2005) and Vangeneugden et al. (2014). The findings of this study indicate that the right pSTS subserves the coding of dynamic social information, such as emotion, conveyed by the body movements of another person.

Previous work has shown that 1 Hz rTMS to the pSTS region can impair discrimination of biological motion from noise (Grossman et al., 2005). Additional work has indicated that rTMS to the pSTS can decrease walking direction discrimination from biological motion while leaving facing orientation unaffected (Vangeneugden et al., 2014). Taken together, these studies underscore the importance of a subregion of the pSTS to the detailed visual processing of biological motion; however, it remains unclear whether the causal role of this pSTS region extends to the coding of social information, such as emotion. It is possible that the pSTS serves as a high-level visual processor that is not central to the processing of social meaning from such stimuli. The selectivity of the fMRI response of the pSTS region to the biological motion region does appear to be linked to social abilities (Pelphrey, Morris, & McCarthy, 2004; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004), and even the size and complexity of social networks (Dziura & Thompson, 2014), suggesting a more diffuse role in social cognition. Assessment of right STS grey matter volume further supports the region as a predictor of social cognition, where increased volume has been associated with biological motion discrimination (Gilaie-Dotan, Kanai, Bahrami, Rees, & Saygin, 2013) and social network size (Kanai, Bahrami, Roylance, & Rees, 2012). More recently, an fMRI study showed that the pSTS region is involved in the processing of emotion conveyed by body movements (Goldberg, Christensen, Flash, Giese, & Malach, 2015). Together with the findings of the present study, which demonstrate a causal role in emotion recognition from biological motion, it seems that the visual coding of human movements represents one facet of a broader social cognitive role played by the pSTS region (Allison, Puce, & McCarthy, 2000).

Consistent with a broader social cognitive role of the right pSTS region, this region has also been considered by many as part of a face-processing network (Haxby, Hoffman, & Gobbini, 2000, 2002; Hoffman & Haxby, 2000). The original model by Haxby and colleagues (2000) proposed that the right pSTS represents changeable aspects of the face, such as emotional expression, eye-gaze, and mouth movements, while ventral temporal fusiform cortex represents invariant aspects of faces, such as identity. This model was modified by O'Toole and colleagues (2002), who suggested that the right pSTS might also encode facial identity based on dynamic motion signatures. The pSTS face area (pSTS-FA) overlaps considerably with the pSTS region that represents biological motion (Deen, Koldewyn, Kanwisher, & Saxe, 2015; Engell & McCarthy, 2013; Grosbras, Beaton, & Eickhoff, 2012), and a causal role for the pSTS-FA in recognizing facial emotional expressions has been demonstrated using rTMS by Pitcher and colleagues (2014). Recent work by Deen et al. (2015) reported functional overlap between STS modules that respond selectively to biological motion and face stimuli; however, reliable differences in the spatial distribution of these modules were also observed. In future work, it will be important to determine the degree of overlap between pSTS modules that exhibit response selectivity for biological movement, emotional expression derived from said motion, and facial expression.

Dysfunction of the processing of biological motion in the right pSTS region has been suggested to be a potential diagnostic "biomarker" for social communication deficits in ASD (Björnsdotter et al., 2016), and it has been implicated in social deficits in schizophrenia (Kim et al., 2013). Our finding of a causal role of this region in emotion recognition from biological motion in healthy adults strengthens the rationale for examining right pSTS functionality when determining the basis of social and emotional deficits in clinical populations. It should be noted that, while we did not examine the potential role of the left pSTS in emotion recognition from kinetic movement, functional connectivity analyses suggest that this region coactivates with the right pSTS in response to social stimuli (Lahnakoski et al., 2012). Further examination of the causal role of the left pSTS in emotion perception is warranted. In pursuing this work,

findings will provide a neurobiological basis to guide future treatment interventions for social and affective processing.

ACKNOWLEDGMENTS

This work was supported by Office of Naval Research Award N00014-10-1-0198.

AUTHOR CONTRIBUTIONS

RAB, MW, and JCT designed the study. RAB and MLW carried out the experimental procedures and completed data analysis. RAB and MLW drafted the manuscript. JCT and MW provided critical feedback on the manuscript, and all authors contributed to the final draft of the manuscript.

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