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The responsiveness of biological motion processing areas to selective attention towards goals

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ABSTRACT

A growing literature indicates that visual cortex areas viewed as primarily responsive to exogenous stimuli are susceptible to top-down modulation by selective attention. The present study examines whether brain areas involved in biological motion perception are among these areas—particularly with respect to selective attention towards human movement goals. Fifteen participants completed a point-light biological motion study following a two-by-two factorial design, with one factor representing an exogenous manipulation of human movement goals (goal-directed versus random movement), and the other an endogenous manipulation (a goal identification task versus an ancillary color-change task). Both manipulations yielded increased activation in the human homologue of motion-sensitive area MT+ (hMT+) as well as the extrastriate body area (EBA). The endogenous manipulation was associated with increased right posterior superior temporal sulcus (STS) activation, whereas the exogenous manipulation was associated with increased activation in left posterior STS. Selective attention towards goals activated a portion of left hMT+/EBA only during the perception of purposeful movement—consistent with emerging theories associating this area with the matching of visual motion input to known goal-directed actions. The overall pattern of results indicates that attention towards the goals of human movement activates biological motion areas. Ultimately, selective attention may explain why some studies examining biological motion show activation in hMT+ and EBA, even when using control stimuli with comparable motion properties.

Introduction

Posterior regions of the brain contain discrete areas involved in processing information about biological motion. The development of these areas has presumably served a critical evolutionary purpose—the identification and classification (predator, prey, kin) of moving animals. This capacity has reached its apogee in humans, where the perception of coherent body movement can provide exquisitely subtle information regarding other people's thoughts and intentions.

It is therefore not surprising that a number of basic visual information processing areas have been implicated in social perception. These areas include the human homologue of non-human primate area MT+ (hMT+). Because this area is active during the passive viewing of a variety of coherent motion stimuli (checkerboards, radial motion displays, random dot kinematograms, human movement, etc.), it is typically construed as a "bottom-up" processing area—i.e., responsive primarily to exogenous (stimulus-driven) visual events (Blake and Shiffrar, 2007; see Sani et al., 2010, for a consideration of hMT+ in the tactile experience of coherent motion). However, numerous studies show increased activation in this area for stimuli depicting biological motion relative to stimuli that share many critical movement parameters (global motion, velocity, etc.; Beauchamp et al., 2002; Grossman and Blake, 2002; Herrington et al., 2011a; Michels et al., 2005, 2009; Peelen et al., 2006; Pelphrey et al., 2004; Peuskens et al., 2005). Some of these studies do not refer to observed activation as encompassing hMT+, despite overlapping directly or extremely closely with hMT+ coordinates reported in multiple studies (for a consideration of hMT+ localization, see Dumoulin et al., 2000). The failure of biological motion studies to more clearly account for activation in this region likely reflects the fact that it is not a discrete functional module with respect to human movement.

However, accumulating evidence indicates that, although not a biological motion module per se, hMT+ may play an important role in human movement processes. For example, Herrington et al. (2011a) recently showed increased hMT+ activation for human movement stimuli compared to a control stimulus (a spinning wheel, which shared many critical motion parameters but differed in the complexity of configural motion). Using an fMRI adaptation paradigm, Jastorff et al.

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(2009) associated hMT+ function with the discrimination of subtle changes in otherwise comparable human movement stimuli. Changes in hMT+ connectivity during biological motion perception have also been reported. For example, Nummenmaa et al. (2010), found increased connectivity between hMT+ and posterior superior temporal sulcus (pSTS, discussed below) during the perception of changes in eye gaze. Nummenmaa et al.'s finding suggests that hMT+ may support biological motion perception by providing motion information to pSTS. It is possible that a low-level visual information processing system such as hMT+ is differentially recruited for specific higher-order tasks that require the discrimination of subtle motion parameters (i.e., human movement perception). This possibility is the focus of the present study; are basic visual information processing systems responsive to selective attention towards the meaning of human movement, even when controlling for visual input to those systems?

hMT+ is one of a number of posterior visual areas shown to be active during human movement perception. It is directly adjacent to the extrastriate body area (EBA), which is responsive to both static and dynamic visual displays of the human form, as well as affordances of human forms (such as tool movement; Beauchamp et al., 2002, 2003; Downing et al., 2001; Grossman and Blake, 2002; Grossman et al., 2004; Michels et al., 2005, 2009; Santi et al., 2003; Spiridon et al., 2006; Wiggett and Downing, 2011). EBA may in fact respond in an obligatory way to human form input (see Jastorff and Orban, 2009). The spatial and functional distinction between EBA and hMT+ has been a recurring theme in the EBA literature since its inception (Downing et al., 2001, 2007; Peelen et al., 2006; Wiggett and Downing, 2011). EBA is often distinguished from hMT+ by virtue of its sensitivity to the static structural components of the human form (whereas hMT+ appears sensitive to dynamic human motion vectors; Downing et al., 2006). Although the case for the hMT+/EBA distinction has been clearly made, EBA has been shown to overlap spatially with hMT+ at the voxel level, to the point where the two areas can be difficult to separate even on a per-subject basis (Downing et al., 2001, 2007; Peelen and Downing, 2007; Peelen et al., 2006; Wiggett and Downing, 2011). Coordinates reported for EBA and hMT+ are in fact highly interdigitated between biological motion studies (for example, EBA coordinates from the references cited above are comparable to hMT+ coordinates from Michels et al., 2005; Peuskens et al., 2005; Spiridon et al., 2006). The spatial and functional relatedness of EBA and hMT+ suggests that, despite the fact that EBA does not appear to play a specific role for biological motion processes as distinct from general human form perception, they may nevertheless work in a coordinated manner during biological motion perception.

A third area – pSTS – shares functions associated with both hMT+ and EBA. PSTS appears selective for the processing of human movement, compared to stationary human forms or non-human movement (for a review see Puce and Perrett, 2003). The proximity of pSTS with hMT+ and EBA, and their co-activation in some biological motion paradigms (for example, Herrington et al., 2011a; Jastorff et al., 2009), suggests that they implement unique but overlapping aspects of human movement perception—hence the term "STS complex" coined by Puce and Perrett (2003; Puce et al., 1998). Although a few studies have examined the respective roles of each area within the complex, the pattern that emerges from the literatures reviewed above suggests that 1) hMT+ processes information related to human configural motion, 2) EBA processes information related to human form, whether moving or not, and 3) pSTS integrates these and possibly other lower-level visual inputs to form the percept of a moving human. Findings on pSTS (but not EBA) suppression during the perception of incongruous motion (i.e., altered videos of one's own movement) suggest that pSTS is integrated with higher order processing structures in a manner that EBA (and by extension hMT+) is not (Kontaris et al., 2009). PSTS thereby serves to integrate visual information processes related to human movement, and to interface with other human movement processing systems during biological motion perception (for example, parietal and frontal motor systems; Carr et al., 2003; Iacoboni et al., 200 l; Kontaris et al., 2009).

It is now widely held that some social information processes may be implemented in part by the STS complex (henceforth called STSC, including pSTS, hMT+, and EBA; Puce and Perrett, 2003). Empirical support for this claim comes from a variety of studies comparing goal-directed human movement to either non-coherent, scrambled motion displays (e.g., Bonda et al., 1996; Grossman and Blake, 2002; Michels et al., 2005; Peuskens et al., 2005; Saygin, 2007; Saygin et al., 2004), or coherent human movement without a salient or predictable goal (Campbell et al., 2001; Pelphrey and Morris, 2006; Pelphrey et al., 2003, 2004; Saxe et al., 2004; Wyk et al., 2009; also see Blake and Shiffrar, 2007). Although it is a widely held view that STSC (particularly pSTS) is involved in the *understanding* of human movement (i.e., Mosconi et al., 2005; Pelphrey and Morris, 2006), a close examination of the paradigms used in this literature reveals some challenges in making this inference. Many studies eliciting robust STSC activation have used human movement stimuli without any manipulation of the endogenous processing of movement meaning or understanding. In other words, whether articulated or not, studies on human movement perception often ignore endogenous processes and assume that human movement processing systems activate in a more or less obligatory manner to the perception of coherent human movement, which is why they are sensitive to basic contrasts of coherent versus non-coherent human movement, or human versus non-human movement. A similar assumption is that these systems will be differentially sensitive to goal-directed movement versus random but legitimate human movement, even when participants are not directed by task demands to attend to goal orientation per se (e.g., Pelphrey et al., 2003, 2004; Saxe et al., 2004).

However, increasing evidence indicates that STS is sensitive to selective attention towards biological motion (Thompson and Parasuraman, 2012). For example, Safford et al. (2010) found increased activation in STS when participants attended to a biological motion stimulus within a display also containing non-biological stimuli (tools). There is also some evidence for attentional modulation of hMT+/EBA. In particular, Luks and Simpson (2004) found increased preparatory activation of hMT+ when prompted to detect the movement direction of a random dot kinematogram before it was actually presented (i.e., in the absence of any visual input). This finding represents very strong evidence that putatively "bottom-up" visual motion areas are modulated by attentional resource allocation. Further evidence also comes from Engel et al. (2008), who found increased activation in the occipito-temporal junction (likely overlapping with hMT+/EBA) during the perception of trained movements (learned immediately prior to scanning), which may relate to heightened attentional resources paid to these movements (in addition to increased input from motor cortices).

The present study tested whether STSC is modulated by selective attention towards or away from the goals of a moving figure (henceforth referred to as goal orientation). Selective attention, in this context, does not refer to attention towards distinct aspects of a single visual display, but to distinct features of a single stimulus (as in, for example, a Stroop task, where selective attention can be paid towards either the color ink or color name of a single word). It is becoming increasingly clear that multiple visual processing areas are modulated by selective attention (Bar et al., 2006; Luks and Simpson, 2004; Miyashita and Hayashi, 2000; Ranganath et al., 2004; Vuilleumier et al., 2001, 2004). However, few studies to date have examined whether STSC and adjacent movement processing areas are among these regions. To our knowledge, no studies to date have tested whether attention to movement goals affects STSC function, independent from changes in perceived stimuli.

This study uses point-light biological motion stimuli to examine the role of selective attention in modulating STSC function. Point-light

biological motion stimuli consist of a series of dots located on the major joints of a human form (13 dots were used here). As first described by Johansson (1973), these dots can appear devoid of any recognizable form when shown statically, but are immediately recognizable as an outline of a human form when set in motion. This property of point-light stimuli indicates that human form information can be derived largely and perhaps entirely by motion information under some circumstances. Point-light stimuli are ideal for research on biological motion perception, as they are easy to manipulate and do not contain any perceptual cues that could inadvertently reveal human form information or motion goals.

The paradigm in this study followed a two-by-two design where goal processing is manipulated according to exogenous (stimulus-driven) and endogenous (task-driven) factors (see Fig. 1). Point-light figures moved in the center of the display in either purposeful (goal-driven, such as digging or swinging a tennis racket) or biologically plausible but purposeless ways (the exogenous manipulation). On a trial-to-trial basis, participants were prompted either to identify the goal of the movement or an ancillary aspect of each stimulus—a color change of two of the 13 dots (the endogenous manipulation). The advantage of this paradigm is that it controls the characteristics of the stimuli presented, basing interpretations of movement judgment on the deliberate application of that judgment. Furthermore, the exogenous manipulation allows for the examination of STSC function as distinct from selective attention (i.e., an examination of bottom-up visual information processing).

The primary hypothesis of this study was that activity within STSC is modulated by both top-down (task-driven) and bottom-up (stimulus-driven) processes related to human movement perception. This hypothesis was tested via the main effects of Stimulus (meaningful versus random point-light figures), Question (goal versus color question), and their interaction. The prediction was that STSC activity would be increased during the perception of goal-oriented versus random stimuli (regardless of question) and for goal-oriented versus non-goal-oriented question (regardless of perceived stimulus). Although this prediction applies to STSC as a network, it is possible that subregions with known functional distinctions (i.e., hMT+, EBA, and pSTS) are differentially sensitive to attention towards goals. In particular, the association between EBA and a wide variety of static human form tasks could arguably lead to the alternative hypothesis that this area will be active in any task where a human form is present, and may therefore be insensitive to goal manipulations.

Materials and methods

Participants

Fifteen adults (7 female, mean/SD age 25.7/4.2) were recruited from the Yale University community to participate in this study. All subjects gave written informed consent in accordance with procedures and protocols approved by the Institutional Review Board of the Yale University School of Medicine. fMRI data for one participant were lost due to computer error. All participants were right-handed and denied a history of head injury, psychiatric disorders or substance abuse. All participants reported normal or corrected-to-normal vision.

Experimental paradigm

In the context of the two-by-two design of the study, goal-directed (GD) and non-goal directed (NGD) stimuli represented the two levels of the Exogenous (stimulus-driven) factor. Nine point-light sequences depicting GD behaviors were taken from a publically available database by Vanrie and Verfaillie (2004). These sequences depict a human figure chopping, digging, drinking, painting, playing tennis, saluting, sawing, stirring, and sweeping. Nine randomly moving NGD point-light figures were derived from those used by Klin et al. (2009). NGD figures appeared to be swaying and/or moving their limbs in a manner that did not appear deliberate. GD and NGD videos were matched on size and mean dot velocity. All point-light stimuli were created by digitizing the locations of joints on actual moving people (i.e., not constructed from computer algorithms). All point-light stimuli were rendered using the Visionegg library for Python (Straw, 2008) and converted to digital videos lasting 2000 ms. Point-light figures were composed of 13 dots presented in frontal view (with the torso parallel to the projection plane), subtending 13.6 and 17.2° of horizontal and vertical visual angles at their maximum (i.e., with arms and legs fully extended). The

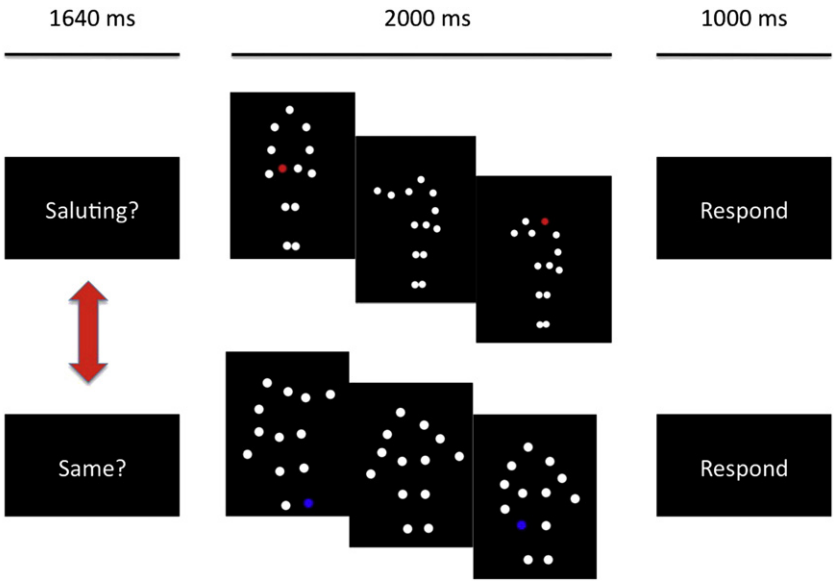

Fig. 1. Task design. This figure contains snapshots of the point-light videos used in the experiment. The paradigm followed a two-by-two design with main effects of Question (goal-focused versus color change-focused) and Stimulus Type (human movement with a clear goal versus plausible but random human movement). The top row depicts a trial that includes a goal-directed animation (saluting), whereas the bottom row shows a randomly moving animation. Goal and color questions were counterbalanced between trial types. This figure is a schematic of the actual stimuli used (the dots here are increased in size, and the figures cropped differently).

central presentation and relatively small size of these stimuli were chosen to minimize the possibility that participants would saccade when completing the paradigm.

The Endogenous factor consisted of the aspect of each video that participants were required to attend to (see Fig. 1). This factor consisted of two levels: goal question (GQ) or non-goal (color) question (NGQ). Prior to each point-light video, a question comprised of a single word was presented on the screen for 1640 ms. In the GQ condition, the question prompted participants to attend to the movement goal (e.g., "Digging?") or to the non-goal aspect of the video. In the NGQ condition, participants were asked about the color of one of the point-light dots. During the first 500 ms of each video, one of the 13 dots (chosen at random) changed color from white to red or blue, then back to white. This happened again during the last 500 ms of each video. If the word "Same?" was presented before the video, participants were to indicate whether the dot changed to the same or different color. All questions therefore followed a two-option forced-choice format (yes or no), where responses were made via button-press (counterbalanced between responses and buttons). All stimuli had this color-dot change, regardless of whether it was to be responded to (NGQ) or not (GQ). Participants were asked to withhold their response until the video was complete, at which point the word "Response" was displayed (1000 ms). Prior to scanning, participants completed a 5-minute practice version of the task (no participants had significant difficulty with the task).

It is important to note that some of the cells in this design were unmatched in certain respects. The goal questions were chosen to involve subordinate (i.e., a choice among goals) rather than basic-level categorization (i.e., goal versus non-goal), as subordinate-level judgments generally involve greater depth of processing. However, no subordinate-level categorization of goal type is possible for a stimulus moving without a discernible goal. For this reason, the correct answer for goal judgments performed on random stimuli was always "no", whereas correct answers were "yes" or "no" for goal stimuli. Although this is a clear difference between the random and non-random stimuli, this difference is not likely to diminish the robustness of the task, as this stimulus manipulation was implicit (the response set, "yes" or "no", was always the same). Even if participants deduced that their response to a random moving stimulus had to be "no" for any given trial, they would have reached this deduction via an analysis of the goal of that stimulus—what the question manipulation was designed to achieve.

A second respect in which cells of the design differed relates to working memory, where the demands presumably differed in kind and possibly in magnitude for the two question types (the color question in fact represents a stimulus matching task). The goal question required participants to match a visual stimulus against a semantic representation of a goal, whereas the color question required participants to match two sequential changes within each stimulus (though the color representation of each color change may have been encoded and retrieved semantically to complete the task). The goal question was chosen instead of an analogous goal-based stimulus matching task in order to avoid the possibility that participants could solve the task based on basic perceptual properties of the stimuli, rather than on the selection of goal representations (the variability in point-light stimulus motion properties and dot distributions is generally much greater between than within goal movement types). A stimulus matching task (such as an N-back task) could have been used for the goal question as well. However, in the present task, it is unclear how the matching of a lexico-semantic representation of an action (i.e., the word "digging") to an actual visual stimulus depicting that action (i.e., a digging point light figure) would yield *more* visual cortex activity than a comparison of two visual stimuli, unless the semantic/visual matching placed increased demands on visual cortex function (i.e., the key experimental manipulation of goal versus non-goal question).

Stimulus presentation followed a pseudorandom event-related design with a trial schedule optimized by the program OptSeq2 (Dale, 1999). Trials were derived from each of the four cells of the two-by-two design (GD/GQ, GD/NGQ, NGD/GQ, and NGD/NGQ), plus null trials (blank screen). Trials lasted a total of 4640 ms, followed by an interstimulus interval of either 0, 2000 or 4000 ms (average = 2000 ms). The experiment was divided into two separate runs, each lasting 10.59 min and containing 91 trials (72 point-light videos, 19 null trials).

Imaging parameters

MRI data were collected using a Siemens Trio 3 T scanner and a CP head coil. During both fMRI runs, gradient-echo echo-planar images were acquired parallel to the anterior and posterior commissures (40 slices, isotropic voxel size = 3.5 mm, TR = 2320 ms, TE = 25 ms, flip angle = 60°). Two structural MRI volumes were acquired for standard-space registration, one acquired in the same plane as the fMRI data (FLASH, .9 × .9 × 3.5 mm, TR/TE = 300/2.46 ms, flip angle = 60°), the other a high-resolution sequence (MPRAGE, 1 mm isotropic resolution, TR/TE = 2530/3.34 ms, flip angle = 7°).

Data reduction and analysis

MRI data were analyzed using BrainVoyager QX (Brain Innovation, Maastricht, The Netherlands). fMRI time series data were motion-corrected, spatially (FWHM = 4 mm) and temporally filtered (linear trend removal). The first four images of each time series were discarded to allow image intensity to reach a steady state. Data were registered into MNI space for visualization and application of masks for family-wise error correction (described below).

Per-voxel GLMs were carried out for each subject using explanatory variables representing each level of the two-by-two design. Explanatory variables modeled the video portion of each trial (i.e., the point-light walker). Vectors representing six motion vectors (three directions of translation and rotation) were included in the GLM as nuisance parameters. Group-level analyses were implemented via a mixed model ANOVA including the random effect of participant.

Family-wise error was controlled using Monte Carlo simulations within masks representing each a priori region of interest[1]. Because of the spatial overlap between reported hMT+ and EBA clusters, a single mask was chosen that encompassed both of these areas (separately for each hemisphere). This mask was derived from the same subjects in this study using a different point-light task (Herrington et al., 2011a) comparing point-light walker to a spinning point-light wheel with similar motion properties. Although pSTS masks were also available from the Herrington et al. (2011a) study, a mask based on the structural anatomy of the posterior and anterior superior temporal sulci was generated using the parcellation scheme implemented by the program Freesurfer (Destrieux et al., 2010), in order to include a larger portion of STS that was structurally defined. The Freesurfer segmentation was run on participant's high-resolution structural MR images; STS output masks were then merged into a single mask. Posterior STS was defined conservatively as the region of STS posterior to the very beginning of the ascent of the Sylvian fissure (y = −30). Lastly, a mask was created encompassing all gray matter areas not included in the aforementioned a priori regions. Because GLMs were carried out at each voxel across the brain, and all gray matter areas were included in the masks, analyses

[1] Secondary hypotheses for this study focused on the amygdala and fusiform gyrus (FG), which have been shown to be modulated by selective attention towards social and affective stimuli (Furey et al., 2006; Herrington et al., 2011a; O'Craven et al., 1999; Vuilleumier, 2002; Vuilleumier et al., 2001, 2004). The family-wise error control procedures used for hMT+/EBA and STS were also used for amygdala and FG. See Supplementary Table 1 for the findings from these areas.

were "whole brain". Per-voxel probabilities for the simulations were set to one-tailed $p < .005$ (the same per-voxel threshold used for all clusters reported in this paper). Cluster sizes corresponding to a corrected $p < .05$ were then chosen for each area. These masks were used for family-wise error correction only; they were not used for ROI analyses that averaged voxels within.

Because hMT+ and EBA overlap spatially, their separate localization presents numerous methodological challenges (see Peelen and Downing, 2007) that were not of direct interest in the present study. For this reason, we report the top three peaks within hMT+/EBA clusters (see Table 1), rather than assigning distinct peaks to hMT+ and EBA.

Post-hoc tests of Question × Stimulus Type interactions were carried out within entire contiguous clusters identified for each main effect, as well as within 6 mm spheres centered on each of the reported peaks. As pSTS showed somewhat different activation patterns between hemispheres (as illustrated in Table 1), post hoc tests of hemispheric asymmetries were carried out as well, comparing parameter estimates for each voxel in the right hemisphere to its contralateral homologue in the left hemisphere (i.e., the voxel in the same position in the anterior/posterior and superior/inferior dimensions, but on the opposite side of midline in the left/right dimension; see Herrington et al., 2010, 2011b). However, none of the pSTS findings proved significantly lateralized at $p < .05$; these results were therefore excluded from the Results section below.

Results

Behavioral performance data

Response time data were not analyzed because participants were asked to withhold responses until after each video was finished. Accuracy was highly comparable across all conditions, $F(3,59) = .66$, n.s. Mean/SD percent accuracy was as follows: GD/GQ = 97.8/3.2, GD/NGQ = 95.7/3.5, NGD/GQ = 96.9/5.44, and NGD/NGQ = 97.0/3.6.

fMRI data

Analyses closely followed the 2 × 2 factorial design of the experiment, with main effects representing Question (goal or color question) and Stimulus Type (goal or random stimuli), and post-hoc tests of Question × Stimulus Type interactions. All significant clusters of activation

Table 1
Significant clusters of activation.

Region	Left hemisphere			Right hemisphere		
	MNI coordinates	Peak Z-value	Size (voxels)	MNI coordinates	Peak Z-value	Size (voxels)
Main effect of Question (goal versus color)						
hMT+/EBA	−41, −67, 4[a]	5.15	4282	37, −70, −3[a]	4.84	4239
hMT+/EBA	−40, −75, −9[a]	4.44	4282	52, −69, 13[a]	4.62	4239
hMT+/EBA	−40, −79, 8[a]	4.50	4282	43, −79, 0[a]	4.12	4239
pSTS				49, −53, 8[a]	5.62	4239
aSTS/MTG				46, −17, −15	4.17	145
Main effect of Stimulus Type (goal versus random)						
hMT+/EBA	−44, −68, 0[a]	6.51	6005	53, −66, 9	5.23	1581
hMT+/EBA	−47, −65, −10[a]	5.77	6005	43, −80, 3	4.83	250
hMT+/EBA	−44, −68, 0[a]	6.51	6005	40, −70, 0	4.11	173
pSTS	−50, −51, 5[a]	4.18	6005			
Simple effect of Question for goal stimuli only						
hMT+/EBA	−45, −76, 11[a]	4.26	1199	55, −65, 9[a]	4.30	1797
hMT+/EBA	−40, −63, −10[a]	4.67	1199	50, −75, 10[a]	4.49	1797
hMT+/EBA	−41, −67, 6[a]	4.12	1199	46, −82, 4[a]	3.62	1797
pSTS	−54, −57, 11	3.45	209			
pSTS/angular gyrus	−60, −53, 22	4.2	195			
Simple effect of Question for random stimuli only						
pSTS				49, −50, 8	5.89	325
aSTS				46, −14, −15	6.22	688
Simple effect of Stimulus Type for goal question only						
hMT+/EBA	−47, −55, 2[a]	5.05	4847	43, −80, −3	5.41	265
hMT+/EBA	−44, −68, 0[a]	4.82	4847	49, −75, 13	4.66	189
hMT+/EBA	−44, −65, −10[a]	3.95	4847			
pSTS	−50, −50, 22	3.93	322			
Supramarg. gyrus/SPL	−28, −48, 38	5.10	1328			
Simple effect of Stimulus Type for color question only						
aSTS				46, −14, −18	4.51	173
Question × Stimulus Type interactions within main and simple effect clusters						
hMT+/EBA	−41, −67, 4	1.82	NA[b]			
pSTS				46, −17, 15	2.23	NA[b]

Note. All clusters were significant at $p < .05$ (corrected for multiple comparisons). MNI coordinates represent peak voxels for each cluster. EBA: extrastriate body area. pSTS: posterior superior temporal sulcus. aSTS: anterior superior temporal sulcus. SPL: superior parietal lobule.

[a] Because of the complexities of distinguishing between hMT+ and EBA, the top three peaks within clusters encompassing these regions are listed, unless distinct peaks in the immediate vicinity of hMT+/EBA could be identified (for example, in the right hemisphere hMT+/EBA cluster for the simple effect of Stimulus Type/goal question map, as this cluster was relatively small and focal). Where present, posterior STS portions of the cluster are also listed as a separate peak. The cluster sizes represented for each peak represent the entire contiguous cluster (encompassing all 3 peaks).

[b] These results were derived from 6 mm spherical ROIs (see the Materials and methods section).

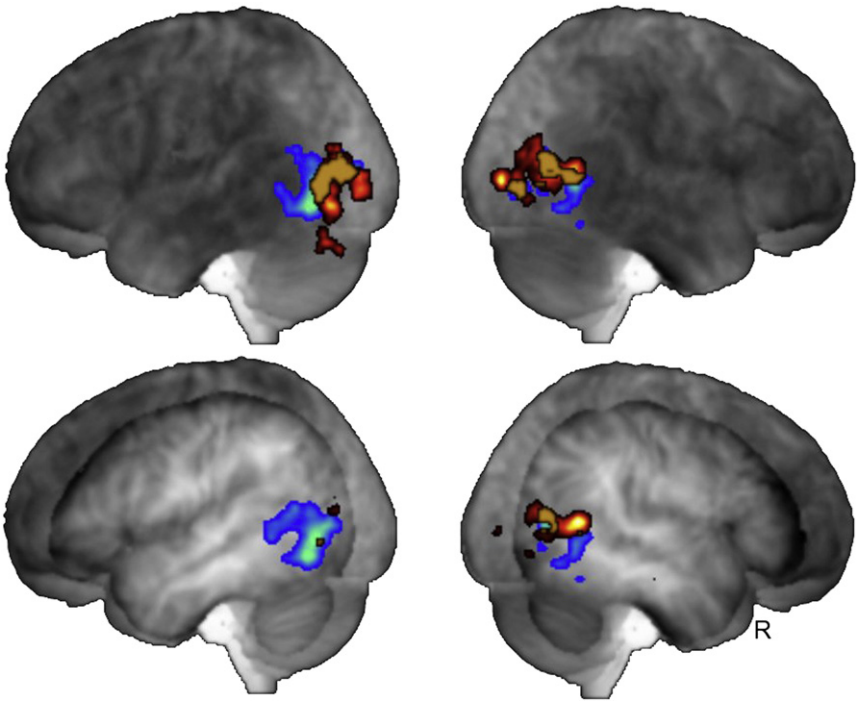

Fig. 2. Main effects of Question and Stimulus. Areas responsive to Question (goal > color) are in red. Areas responsive to Stimuli (goal > random) are in blue. Areas where these overlapped are in gold. The top left and right panels show hMT+/EBA activation projected onto the outer surface of the brain in the left and right hemispheres (respectively). The bottom left and right panels cut into the temporal lobes to illustrate protrusions of these clusters into posterior STS. All clusters are significant at a family-wise error corrected threshold of $p < .05$.

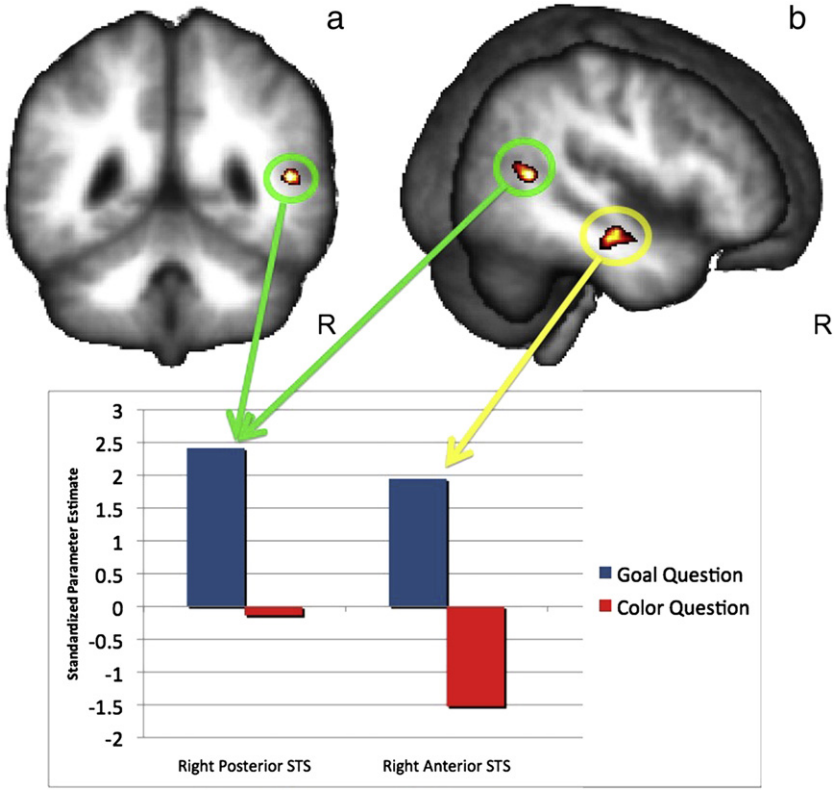

Fig. 3. Simple effect of Question (goal > color) for random stimuli. Panel a: clusters in posterior (circled in green) and anterior (circled in yellow) STS. Panel b: coronal view of posterior STS cluster (circled in green). All clusters were significant at a family-wise error-corrected threshold of $p < .05$. Boxplots below each picture show averaged standardized parameter estimates (z-values) associated with each level of each contrast (compared to rest).

within STSC and adjacent areas are listed in Table 1 (data on fusiform gyrus and amygdala activation are provided in Supplementary Table 1). All coordinates listed are in MNI space.

Main effect of Question

Participants showed significantly increased activation in hMT+ and EBA bilaterally when responding to the question about stimulus goal versus stimulus color (collapsing across goal and random stimulus types; see Table 1 and Fig. 2). The left hemisphere cluster extended inferiorly into the fusiform gyrus. Activation extended partially into pSTS in the right hemisphere. A significant cluster of activation was observed deep within right anterior STS and middle temporal gyrus (MTG; peak coordinates = 46, −17, −15, $p < .001$). No other clusters of activation were observed at family-wise error-corrected significance thresholds.

Main effect of Stimulus Type

The Stimulus manipulation (goal > random movement) yielded a similar pattern of activation as the main effect of Question—significantly greater activation in hMT+ bilaterally (see Table 1 and Fig. 2.). These clusters overlapped substantially with those from the Question map, though not completely. Activation included pSTS in the left hemisphere only (peak coordinates = −50, −51,5, $p = <.001$).

Simple effects of Question for goal and random stimuli

Post-hoc simple effects tests examined whether the effect of Question might be observed more clearly during one stimulus type only (i.e., when observing goal or random stimuli). Activation within hMT+/EBA was observed bilaterally. Significantly increased activation for left pSTS was observed for goal questions only when viewing goal stimuli (−54, −57, 11, $p < .001$). Interestingly, this simple effects test did not show increased activation in right pSTS, despite the presence of a Question main effect in this area. As for the simple effect of Question for random stimuli, only activation of right STS was observed (see Fig. 3); the bilateral hMT+/EBA activation found in the Goal Stimulus simple effect map was absent. The right STS activation included two distinct STS clusters, one posterior (49, −50,8, $p < .001$), the other anterior (46, −14, −15, $p < .001$). This simple effect map also showed that the right anterior STS cluster shown in the Question main effect map (described above) was driven primarily by a Question effect for random stimuli and not goal stimuli. The most significant result from these simple effects analyses was that the main effect of Question within hMT+/EBA was driven primarily by the goal stimulus condition but not the random stimulus condition.

Simple effects of Stimulus Type for goal and color questions

Separate simple effects tests were also carried out to examine the effect of Stimulus Type at each level of the Question factor. Bilateral hMT+/EBA activation was observed when participants made goal judgments on goal versus random stimuli (see Table 1). This analysis also yielded activation in left pSTS (−50, −50, 22, $p < .001$) and left supramarginal gyrus/superior parietal lobule (−28, −48, 38, $p < .001$). Only one cluster of activation was observed when participants made color change judgments on goal versus random stimuli—within right anterior STS (46, −14, −18; $p < .001$). The overall pattern suggested that the observed main effect of Stimulus Type for left pSTS was driven primarily by data from the goal question but not the color question condition.

Question × Stimulus Type interactions

A portion of left hMT+/EBA showed a significant effect of Question when perceiving goal stimuli, but not random stimuli. A cluster within anterior STS showed this same pattern. The ideal way to test that Question effects in these areas were specific to goal stimuli was to examine the Question × Stimulus Type interaction (in the context of the omnibus two-way ANOVA including these factors). The Question × Stimulus Type interaction was tested within each main effect cluster and within 6 mm spheres drawn around each reported peak. One significant interaction and one statistical trend were noted when using the spherical approach. The statistical trend was centered on hMT+/EBA (−41, −67, 4; $p = .069$), where the interaction was driven by significantly increased activation for the Goal Question/Goal Stimulus condition versus the Color Question/Goal Stimulus condition (the simple effect of Question for the random stimulus condition was not significant). Although not significant at $p < .05$, the interaction pattern indicates that this portion of hMT+/EBA is particularly responsive to selective attention towards goals when perceiving goal-oriented stimuli. Second, a significant interaction was observed in right anterior STS (46, −17, −15, $p = .026$), driven by increased activation when attending to goals for random stimuli only. No other significant interactions were noted that reached trend level.

Discussion

Overview of findings

The present data establish that visual motion areas are modulated by selective attention towards the goals of a moving human form. Attention to movement goals versus an ancillary color change was sufficient to yield increased activation in brain areas responding to human movement, even when perceiving identical stimuli in goal and non-goal conditions.

STSC proved sensitive to both bottom-up and top-down manipulations of goal salience. The bottom-up (exogenous) responsiveness of the system is consistent with a large number of biological motion studies where no explicit assessment of movement goals is required (e.g., Bonda et al., 1996; Campbell et al., 2001; Michels et al., 2005; Pelphrey and Morris, 2006; Pelphrey et al., 2003, 2004; Peuskens et al., 2005; Saxe et al., 2004; Saygin, 2007; Saygin et al., 2004; Wyk et al., 2009). The present study extends these findings by demonstrating that effects of selective attention (endogenous, top-down processing) are superimposed on these bottom-up processes (Blake and Shiffrar, 2007). This is consistent with the emerging view that putatively basic visual motion systems are regulated by attentional biases and attentional set (Bar et al., 2006; Luks and Simpson, 2004; Pessoa, 2005).

Although main effects revealed findings regarding STSC as a whole, a number of distinct patterns were observed within STSC that critically inform how we interpret the role of selective attention in modulating this region. In particular, a portion of hMT+/EBA was more responsive for the Question manipulation when perceiving goal stimuli only (a Question × Stimulus Type interaction). Although the *p*-value associated with this effect was only .069, it appears likely that the result would achieve statistical significance in a larger sample. The general pattern of this result suggests that attention may have a particular role in modulating hMT+/EBA function when perceiving stimuli that move with a clear goal. This is an intriguing finding with few direct precedents in the literatures on either hMT+ or EBA.

hMT+, EBA, and the understanding of purposeful human movement

The present findings have implications for our understanding of the unique and overlapping information processes implemented by hMT+ and EBA. The most parsimonious interpretation of the effect of selective attention on hMT+ relates to the highly configural nature of human movement. Although the color question required participants to evaluate the entire point-light display (the locations of the dots changing color were chosen randomly), the goal question alone required participants to integrate the information in the display. Findings from this study strongly indicate that the interpretation of goals from human movement rely on the active recruitment of coherent motion processing centers.

The interpretation of the present findings for EBA function, on the other hand, needs to account for the fact that this area has proven responsive to a variety of *static* as well as dynamic representations of human forms, irrespective of the presence or absence of obvious movement goals. Although EBA typically appears broadly tuned to human form perception, some studies suggest that EBA responsiveness may be more constrained than previously thought. For example, using a series of experimental manipulations of point light shape, kinematics, and attentional load, Jastorff and Orban (2009) reported that EBA may serve a specific role for action recognition, integrating action cues (shape, motion, etc.) and linking "the portrayed action with the body" (p. 7327). With this in mind, one interpretation of the present Question × Stimulus Type trend within hMT+/EBA is that the linking of action to stimulus was more likely to occur when focusing on the goals of a stimulus that was moving with a clear goal. In this context, it is important to note that the interaction trend does not imply that hMT+/EBA activation was inactive during the perception of randomly moving stimuli, but rather, that the measured activity during random stimulus trials did not vary as a function of question type (whereas it did vary for goal stimuli).

This interpretation fits EBA but not hMT+ per se (Jastorff and Orban used functional localizers to isolate these areas; 2009). Although the respective locations of hMT+ and EBA were not isolated in the present study, the size and position of the main effect clusters (Fig. 2) suggest that these two areas are simultaneously active during some types of goal judgments. It should be noted that this does not mean that the functions implemented by each of these regions are reducible to one another, or that there are no spatial distinctions between them. Because of the limits of fMRI spatial resolution, examinations of unique and overlapping hMT+ and EBA areas are difficult to implement. Recently, multivariate pattern analysis (MVPA) has been used to sidestep some aspects of the spatial resolution limitation within visual cortex (see Grill-Spector et al., 2006; Norman et al., 2006; Peelen et al., 2009; Wiggett and Downing, 2011). A clear next step in this line of research is to use techniques like MVPA in conjunction with MRI sequence parameters that are tuned to maximize spatial and temporal resolutions within STSC (for example, foregoing full-head coverage to minimize voxel size and sample rate).

STS and the perception of ambiguous human movement

hMT+/EBA was selective for goal question only when viewing stimuli that had a clear goal. Right pSTS, on the other hand, was selective for goal questions only when stimuli were moving randomly. Although preliminary, these data raise the intriguing possibility that right pSTS plays a particular role in the interpretation of human movement when that movement is ambiguous. A portion of right anterior STS showed this same pattern (increased for the goal question condition when perceiving random stimuli). Although there are few theoretical treatments of what accounts for variations in activation clusters along the length of STS (other than body-part specific areas), the present findings are consistent with multiple studies reporting activity in anterior STS during biological motion tasks (see Puce and Perrett, 2003; also see Herrington et al., 2011a).

There are at least two related mechanistic accounts of why randomly moving stimuli elicit greater attentional modulation of right pSTS. One focuses on resource allocation and task difficulty; it is possible that this portion of right pSTS is simply more active for tasks that tax biological motion processes, and that these processes were not heavily taxed when making a goal judgment on highly salient human motion. Although accuracy effects were close to ceiling for all conditions, response time data may have shed light on this possibility, had the paradigm allowed for this analysis (see the Materials and methods section). A more specific account focuses on the putative role of STS as a convergence zone between visual and motor representations of human movement (Boussaoud et al., 1990; Felleman and Van Essen, 1991; Milner, 2006; Oram and Perrett, 1996). There has been some speculation that pSTS may function as a "comparator" reconciling observed visual movement with efferent motor plans (Carr et al., 2003; Iacoboni et al., 2001). It is thereby possible that pSTS activation varies with the discrepancy between observed and known movements. Because most point-light studies confound exogenous and endogenous goal manipulations (see the Introduction), there are presently few data that could be used to confirm the general findings for right pSTS or speak to either of these two accounts—clearly an area for continued research.

Interestingly, left and right pSTS showed distinct patterns of responsiveness to both the exogenous and endogenous task manipulations. Whereas right STS was significantly more responsive to selective attention to goals when perceiving random stimuli, a portion of left STS was significantly more responsive to goal attention when perceiving coherent stimuli. Furthermore, left pSTS, but not right, was significantly more active for goal stimuli when attending to color change. Although none of the pSTS regions reached statistical significance on post hoc tests of hemispheric asymmetry, the overall pattern of asymmetry is intriguing. One possible interpretation is that right hemisphere pSTS is more specialized than the left in completing more challenging or ambiguous biological motion tasks. While there appear to be no precedents for this result in the existing biological motion literature, it is broadly consistent with more general findings of right hemisphere specialization for some aspects of biological motion processing, insofar as more challenging or ambiguous biological motion tasks may require greater depth of processing (Corballis, 2003; Decety and Lamm, 2007; Grosbras et al., 2012; Herrington et al., 2011a).

Most of the observed STS activation difference was constrained to posterior areas (consistent with the majority of point-light biological motion studies). However, a right anterior STS region was significantly more active for goal questions across stimulus types. Post hoc testing revealed a significant Question × Stimulus Type interaction whereby this cluster showed significantly increased activation in response to goal questions for random stimuli, but not for goal stimuli. At least two interpretations of this finding are possible. First, as described above with pSTS, it is possible that activity in this anterior STS area reflects task difficulty. A second interpretation is related but distinct—that this portion of STS registers a mismatch between observed and recognized goal-oriented movements.

Conclusions and future directions

The primary objective of this study was to establish the sensitivity of STSC to selective attention towards human movement goals. Upon establishing this sensitivity, a number of interesting questions emerge. Many of these questions relate to the internal organization of STSC. Although our STSC findings are consistent with multiple prior studies using biological motion stimuli, this does not imply that the three areas comprising STSC represent one information processing module. As reviewed in the Introduction, the three constituents of STSC are functionally distinct—one sensitive to human form information (EBA), a second sensitive to coherent motion (hMT+), and a third sensitive to biological motion (pSTS). Research on the relationships between these areas can directly inform our understanding of how humans have developed a specialization of biological motion perception.

Examinations of network behavior between these structures, and between STSC and cognitive control regions, may prove especially fruitful. In light of the present data, there are at least two general networks that would be valuable to consider. The first network consists of the constituents of STSC, including hMT+, EBA, and pSTS. Research in this vein would likely require the use of independent localizers to identify unique portions of each region. One general prediction would be that feedforward visual input from hMT+ and EBA

modulates pSTS during human movement perception (Lange and Lappe, 2006; Thompson et al., 2005). A second network would include selective attention and cognitive control structures that may be responsible for the up-regulation of STSC when focusing on movement goals. The present paradigm was not particularly well suited to isolating general mechanisms of selective attention, as these mechanisms were presumably active during both question conditions (goal and color). Some areas of activation for goal versus color question were observed in inferior and middle frontal gyri, but these did not survive family-wise error-correction. Dorsolateral prefrontal and anterior cingulate cortices may ultimately play a role in the observed STSC modulation, as these areas have been implicated in goal and attentional set maintenance during tasks with multiple stimulus/response parameters (Banich et al., 2000a, 2000b; Milham et al., 2003).

Future studies in this area would benefit from measures of spatial attention that were not included here. A key design advantage of the present study is that selective attention to stimulus goals was manipulated independent of the type of stimulus presented. Furthermore, information regarding the two question types (goal or color) was spatially coincident, minimizing the influence of covert spatial attention (which has been shown to influence visual cortex activation in some studies; Brassen et al., 2010; Moore et al., 2003). However, this by itself does not guarantee that the information arriving at the visual cortex was identical across goal and color question conditions, or that the visual space was attended to identically. Specifically, it is possible that selective attention differentially influenced eye gaze strategies for each condition. Although eye tracking data were recorded for the first few participants in this study, it was discontinued, as it did not appear that participants were making any saccades away from the screen center (consistent with the configural nature of the stimuli, their relatively tight distribution, and the random locations of the color dots). Furthermore, the absence of significant activation differences in key eye control regions argues against attention-based differences in gaze strategy. Nevertheless, the addition of eye tracking measures and/or spatial attention manipulations would further our understanding of the precise role of goal orientation on STSC function.

It is also important to note that, while the present design included conditions that were well matched in terms of the primary parameter of interest (goal versus non-goal dimensions), they differed in other respects that could be factored into future studies. In particular, the goal and random stimuli in this study differed in the use of transitive actions; whereas most goal-directed human movements involve manipulations of objects, few random movements are likely to do so. Although transitive and intransitive movements have been shown to elicit some differences in brain activation, these differences are generally associated with somatosensory (parietal) areas and higher-order information processing centers (i.e., prefrontal cortex; Buxbaum et al., 2007; Króliczak and Frey, 2009). One general prediction is that attention to the goals of transitive and intransitive actions will modulate STSC (for data in support of this view see Villarreal et al., 2008). This would be most directly tested using a paradigm that manipulates selective attention towards goals while including meaningful, non-transitive human motion (of which human gestures are the primary exemplar).

In summary, the present data indicate that areas of the brain that are sensitive to basic visual motion parameters can be selectively recruited to complete higher-order social information processing tasks. This observation has implications for our understanding of abnormal as well as normal psychological processes. For example, autism spectrum disorder (ASD) is associated with diminished social information processing abilities as well as decreased social motivation (Chevallier et al., 2012). Deficits in STSC and related visual processing centers have been widely observed in this population (Herrington et al., 2007; Pelphrey and Carter, 2008; Schultz et al., 2000; Zilbovicius et al., 2006). Findings from the present study suggest that visual information processing deficits in ASD may stem for a cascade of visual cortex deficits, extending from basic to higher-order processing centers.

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