PERGAMON

Vision Research 41 (2001) 1475–1482

Vision Research

www.elsevier.com/locate/visres

Brain activity evoked by inverted and imagined biological motion

E.D. Grossman *, R. Blake

Department of Psychology/Vanderbilt Vision Research Center, Vanderbilt University, Nashville, TN 37240, USA

Received 25 July 2000; received in revised form 13 December 2000

Abstract

Previous imaging research has identified an area on the human posterior superior temporal sulcus (STS) activated upon viewing biological motion. The current experiments explore the relationship between neural activity within this region and perceptual experience. Biological motion perception is orientation dependent: inverting point-light animations make them more difficult to see. We measured activity levels within this region as observers viewed inverted point-light animations. We also measured neural activity while observers imagined biological motion and compared it to that measured while observers viewed the animations. In both experiments we found that the BOLD response was modulated with perceptual experience. Viewing inverted biological motion activated posterior STS more than scrambled motion, but less than upright biological motion. Mental imagery of biological motion was also sufficient to activate this region in most of our observers, but the level of activity was weaker than during actual viewing of the motion animations. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Motion perception; Biological motion; Functional imaging; Mental imagery

1. Introduction

Modern brain imaging techniques have revealed multiple brain areas involved in perception of visual motion. According to one account, there exist more than a dozen distinct neural regions responsive to visual motion stretching from the occipital lobe to the frontal lobe (Sunaert, Van Hecke, Marchal, & Orban, 1999). Prominent among these motion-responsive regions are area V1 (which responds to almost any moving pattern as well as to flicker), the MT/MST complex which responds weakly to flicker but strongly to coherent motion including optic flow patterns (Watson et al., 1993; Dupont, Orban, De Bruyn, Verbruggen, & Mortelmans, 1994; Cheng, Fujita, Kanno, Miura, & Tanaka, 1995; Tootell et al., 1995), and area KO, or LOC/LOP as it is sometimes called, which responds preferentially to motion-defined boundaries (Malach et al., 1995; Orban et al., 1995; Van Oostende, Sunaert, Van Hecke, Marchal, & Orban, 1997).

Of course, one of the most biologically salient forms of visual motion for an observer is associated with viewing the activities of other people. Several groups have used fMRI and PET to identify brain regions uniquely activated by biological animations portrayed by point-lights (Bonda, Petrides, Ostry, & Evans, 1996; Howard et al., 1996; Grossman et al., 2000). With these novel animations, the activity and identity of an animate creature are compellingly created using just a dozen or so light points strategically placed on the individual's body (Johansson, 1973). Perception of animate motion in these displays must entail global integration of these motion signals over space and time (Ahlström, Blake, & Ahlström, 1997). Consistent with neuropsychological findings from brain-damaged patients (Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990; Schenk & Zihl, 1997a,b; Cowey & Vaina, 2000), our recent fMRI results identified a region on the posterior superior temporal sulcus (STS) active during viewing of biological motion, but not active when viewing animations containing the same local motion vectors scrambled in space. This region lies anterior and superior to area V5, the human analog to MT/MST, and anterior and inferior to area KO, a brain region selectively activated by kinetic boundaries (Malach et al., 1995; Orban et al., 1995).

* Corresponding author. Fax: +1-615-3435027.
E-mail address: e.grossman@vanderbilt.edu (E.D. Grossman).

PII: S0042-6989(00)00317-5

Our earlier work set the stage for examining the extent to which STS is uniquely activated by biological motion events and for determining the necessary stimulus conditions for that activation. To get at these questions, we measured BOLD responses (and, by inference, neural activity; e.g. Rees, Friston, & Koch, 2000) within posterior STS while observers viewed upright and inverted biological motion sequences. It is known that inverting the point light figure makes biological motion more difficult to see (Sumi, 1984; Ahlström et al., 1997; Pavlova & Sokolov, 2000). Are corresponding differences found in STS activation when observers view upright and inverted sequences?

In a related vein, we measured STS activation while experienced observers imagined biological events signaled by verbal instruction. Other fMRI work (Kourtzi & Kanwisher, 2000) has revealed activation in visual area(s) MT/MST when observers viewed static pictures of individuals engaged in activity, but not when observers viewed pictures of people at rest. Kourtzi and Kanwisher speculated that this activation of MT/MST to 'implied motion' could reflect feedback from higher visual areas responsible for registering human activity. Area STS, of course, is a prime candidate for such a mechanism, and the work described here tests whether STS can indeed be activated by imagination.

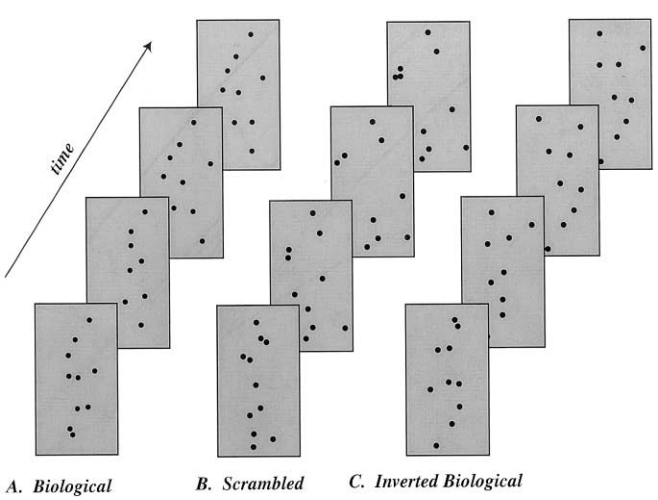

Fig. 1. Four frames of a point-light walker as used in the upright, inverted and scrambled motion conditions. (A) The upright point-light walker in mid-gait. The figure is facing rightward, but there is no translation in the animation. Because of the natural occlusions created by the body, only 10 point-lights are needed to see the figure. (B) Scrambling the starting position of the dots destroys the perception of biological motion even though the local motion vectors are left intact. (C) Inverting the point-light display makes it difficult for naive observers to discern the animations as biological.

2. Methods: general aspects

2.1. Stimuli

Observers viewed biological motion sequences containing all the natural movements and occlusions present in human movement. These sequences were created by appropriate placement of 12 dots on the limbs and head of an actor engaged in various activities including jumping, kicking, running and throwing (see Fig. 1; Ahlström et al., 1997). Animations were displayed using either Matlab together with routines from the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) or EPrime (Psychological Software Tools, Inc.). All dots were black against a gray background, and subtended approximately 12 arc min of visual angle. The entire point-light figure subtended approximately $3.0 \times 6.0°$ of visual angle. Animations consisted of 20 frames displayed over a 1-s period, followed by a 1-s blank inter-stimulus interval (ISI). At this inter-frame interval, approximately 50 ms, the point-light sequences produced the perception of smooth animate motion.

Scrambled motion sequences were created from the exact same motion vectors found in the biological animations, but with the initial starting positions of the dots randomized (constrained to approximate the dot density of the biological motion figures). This maneuver leaves the motion paths of each joint intact, but destroys the coherent spatial relations among the dots. Scrambled animations resemble a cluster of dots moving at different speeds in various directions, with an overall motion 'flow' in common (corresponding to the net flow of the biological sequence).

2.2. Procedure

Scanning was conducted using a 1.5 Telsa GE Signa MR scanner located in the Vanderbilt University Medical Center. Each experimental session lasted approximately 1 h. Within each session we acquired a set of whole brain high resolution images (spoiled-grass, 60 T1 weighted images, $0.9375 \times 0.9375 \times 2.5$ mm) later used to identify anatomical landmarks. Functional images were acquired using single-shot gradient-recalled echoplanar imaging (EPI, 135 volumes, $TR = 2000$ ms, $TE = 60$ ms, flip angle $= 90°$). We acquired 14 axial slices ($3.75 \times 3.75 \times 7$ mm, 0 mm gap) which sampled the entire brain of most observers. Animations were displayed using a LCD panel (PST, Inc.; 640×480 resolution, 60 Hz) mounted on a birdcage headcoil. An adjustable periscope mirror allowed the observer complete viewing of the display.

Each functional scan lasted 4.5 min, beginning with an initial 8-s period during which observers passively viewed a fixation cross. This 'rest period' allowed for MR saturation, and the volumes collected during this period

were discarded prior to analysis. The remainder of each scan was divided into 16-s phases, alternating between different stimulus conditions. Within each phase, animations were presented every 2 s (1 s animation, 1 s ISI).

2.3. Analysis

Reconstruction and analysis were performed offline on a Silicon Graphics dual-processor SGI Octane using AFNI 2.23 (Cox & Hyde, 1997). Prior to any statistical analysis, the first four volumes of each functional scan were discarded to allow for stabilization of the MR signal. The remaining first volume served as a prototype to which subsequent volumes were aligned, correcting for inplane and across-plane motion. Image sequences were corrected for linear drift, spatially smoothed (7.5-mm FWHM Gaussian kernal) and linearly smoothed over time.

3. Localizer experiment: biological and scrambled motion

The goal of this study is to understand how neural activity within regions implicated in biological motion perception changes as the biological stimulus itself changes. To accomplish this we first must determine, for each observer, the brain regions that respond selectively to biological motion, for these regions will be pinpointed for our subsequent analyses. Our earlier work pointed to an area on posterior STS, but we needed to identify this region in our present group of observers[1]. Thus, in a blocked design we measured BOLD signals associated with viewing of biological motion and compared them to responses associated with viewing scrambled motion. As indicated below, this condition was not always the first scan within the session.

To identify clusters of neighboring voxels (regions of interest: ROI) that responded preferentially to biological motion, observers viewed alternating blocks of biological and scrambled motion (Grossman et al., 2000). Knowing that attention can modulate fMRI signals (e.g. Watanabe et al., 1998), we sought to maintain a fixed level of attention during data collection by employing a 1-back task: throughout the scan, observers pressed a button whenever a 1-s animation was identical to the one seen on the immediately preceding 1-s presentation. Each block contained eight animations, and repeats occurred approximately 50% of the time.

The resulting 135 volumes were cross-correlated with an ideal boxcar function describing the alterations of biological and scrambled motion (lagged 4 s to account for hemodynamic response). The phases of biological and scrambled motion lasted for 16 s and were repeated alternately eight times, resulting in a total of 64 volumes acquired for each stimulus phase. A region on the posterior STS has previously been identified as responding selectively to biological motion (Grossman et al., 2000). Voxels highly correlated with the biological motion phases ($r \geq 0.22$, $P < 0.05$, uncorrected) located on posterior STS were selected as our ROI. The voxels within the ROIs were averaged and the mean activation for the biological and scrambled phases compared. Average activation in response to the biological motion is expressed as percent change from activity levels associated with scrambled motion.

Consistent with previous findings, a region on the posterior STS responded preferentially to biological motion (Fig. 2). We were able to locate voxels activated uniquely by biological motion on the posterior STS in all but one of our 10 observers. Six observers had regions in both hemispheres (bilateral), and three had unilateral regions all in the right hemisphere. None of our observers had unilateral responsive regions in the left hemisphere. This tendency for right hemisphere dominance was also noted in previous reports on this region (Bonda et al., 1996; Grossman et al., 2000).

Having identified the ROI, we were now ready to measure the extent to which the activation in this area is dependent on viewing biological motion in its canonical orientation.

4. Experiment 1: inverted and upright biological motion

The comparison stimulus used in our localizer condition — scrambled motion — lacks the spatio-temporal relations characteristic of the biological animations. Consequently these sequences do not appear biological, even though they contain all the individual motion vectors associated with biological sequences. Turning a point-light animation upside-down maintains the original biological motion vectors and, also, preserves the correct dot relationships specifying hierarchical, pendular motions. Still, inverted sequences are difficult to discern as biological (Sumi 1984; Ahlström et al., 1997; Pavlova & Sokolov, 2000). We exploited this orientation dependence to manipulate the perceptual experience of our naive observers.

In this experiment we asked whether neural activity within a region that responds preferentially to biological motion is affected when an observer views inverted biological motion[2]. In all ways except orientation, the

[1] This is a new group of observers from our previous study (Grossman et al., 2000). As indicated, all the observers from Experiments 1 and 2 participated in this localizer experiment, and because it was critical in Experiment 1 that the observers have minimal prior experience with point-light animations we had to recruit new, naive observers.

[2] Note that this manipulation would not necessarily work with an observer experienced in viewing point-light animations. Once animations become familiar, a simple mental rotation makes the inverted point-light displays relatively easy to recognize as biological. It was for this reason that we used naive observers in Experiment 1.

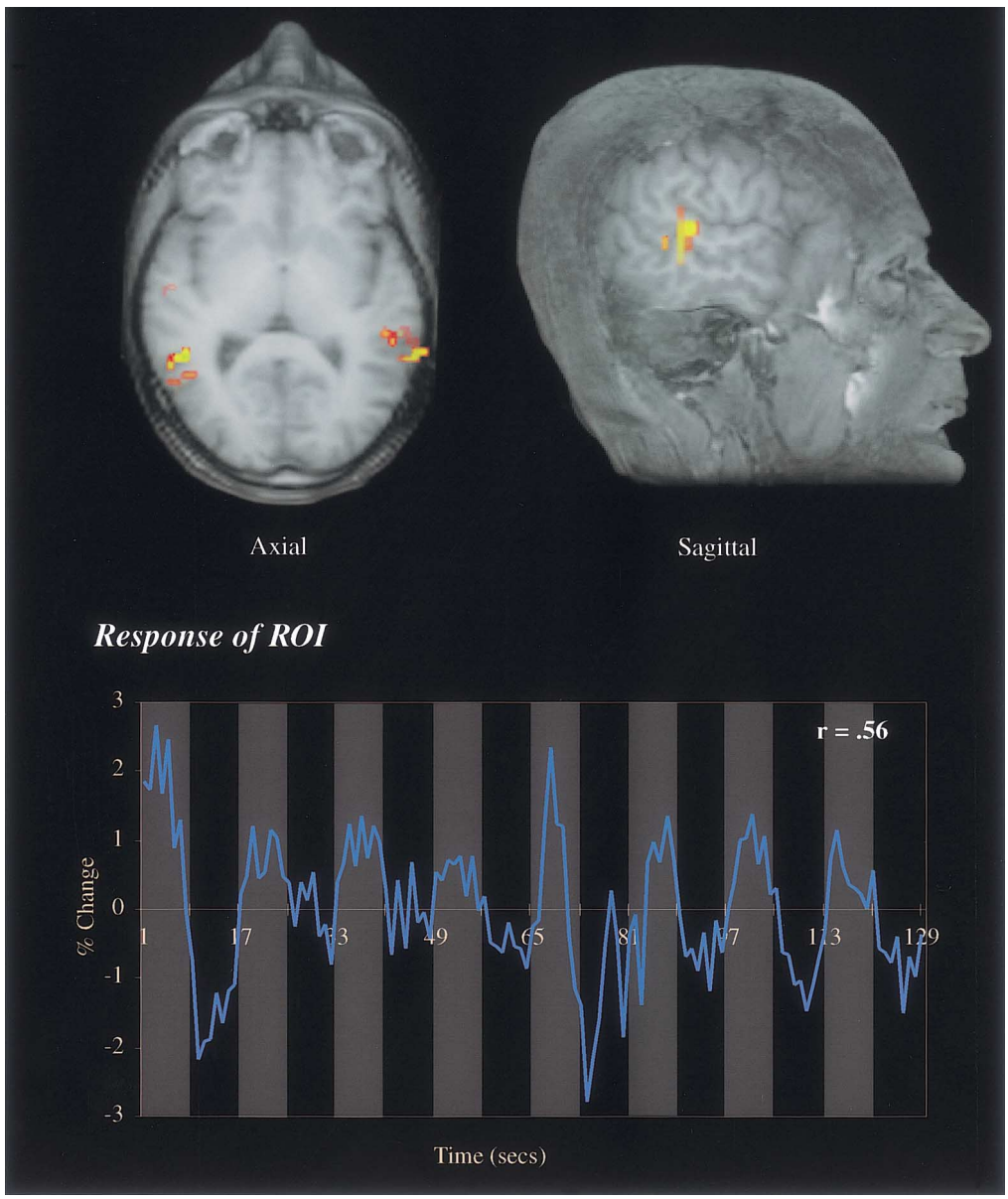

Fig. 2. Axial and sagittal views of the biological motion responsive area on the posterior superior temporal sulcus (STS). This region is anterior and superior to the human MT/MST complex, and anterior and inferior to KO/LO. In this observer (VS) the activation is bilateral, though we find a slight right hemisphere dominance among our observers. The response of the ROI during biological and scrambled blocks is indicated in blue. These regions have higher activity levels when observers see biological motion sequences (light gray bars) than when they view scrambled motion sequences (correlation in this observer $r = 0.56$).

inverted biological motion animations were identical to the upright biological sequences.

4.1. Methods

Eight naive observers (four women, four men) with normal or corrected to normal vision participated in this experiment. When provided verbal descriptions of biological motion portrayed with point-light animation, only one reported any prior experience viewing these unique biological motion sequences. All observers gave informed consent as approved by the Vanderbilt University Institutional Review Board.

Observers viewed alternating phases of upright biological motion, inverted biological motion and scrambled motion. The order of the phases was counterbalanced across observers, and periodic within a scan. Observers were not told anything about the nature of the sequences to be viewed, other than that they would see 1-s presentations of clusters of moving dots. They were instructed to respond when a given presentation was identical to the immediately preceding one (i.e. the 1-back task employed to maintain attention).

Because the orientation manipulation can be affected by experience, this experiment was the first scan of the

session in which observers viewed point-light motion. Analyses were conducted only within the regions that respond preferentially to biological motion. These regions were identified in later scans, during which the observers viewed biological animations alternating with scrambled motion (see above, localizer condition).

A total of 40 volumes were acquired for each of the three stimulus conditions. The volumes during which observers watched scrambled motion were averaged into a single value of baseline neural activity. The average activity levels for the upright and inverted biological conditions are expressed as percent changes from the average scrambled signal.

4.2. Results and discussion

Results from this experiment are summarized in the histograms in Fig. 3. Once again, upright biological sequences reliably produced significant activation in area STS, relative to the scrambled sequences in all of the eight observers ($P < 0.05$). This is not surprising because posterior STS has already been demonstrated to respond selectively to biological motion compared to other kinds of motion, including scrambled motion. Moreover, upright animations produced larger BOLD responses than did the inverted sequences in all but one observer. In six of the observers this effect was statistically significant ($P < 0.05$). On average, the BOLD signal associated with viewing inverted biological motion was about half that associated with viewing upright biological animations (0.33 and 0.79%, respectively); this difference dovetails nicely with the reduced perceptual salience of the inverted sequences. Still, in six of the eight observers, activations in posterior STS were significantly higher in response to inverted biological motion than to scrambled animations ($P < 0.05$). This result is not too surprising to us. In unpublished work in our lab, we have found that people rate inverted sequences as 'more coherent' than scrambled versions of those sequences, so obviously people can discriminate the two classes of animations. Moreover, the naive observers did receive some exposure, albeit minimal, to upright biological sequences during the course of this scanning session. It is conceivable, then, that some of the inverted sequences were recognized as biological. After the session each observer was queried about what he/she saw, and all individuals mentioned seeing some biological motion sequences upside-down.

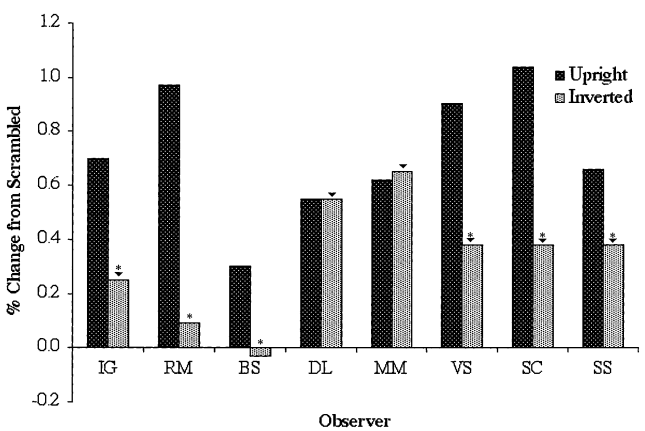

Fig. 3. Percent change of BOLD response during viewing of upright biological motion (dark bars) and inverted biological motion (light bars) for all eight observers. BOLD signal is expressed as a percentage of response from posterior STS to scrambled motion. (▼) Indicates statistically significant differences between the inverted biological motion condition and the scrambled baseline. (∗) Indicates statistically significant differences between the upright biological and inverted biological conditions. The difference in neural activity during upright biological motion and scrambled motion animations was significant in all observers.

During each scanning sequence observers engaged in a 1-back task, our aim being to maintain a fixed level of attention. However, performance of this task does not guarantee that attentional resources were used to the same degree during the different stimulus phases. One could argue that the larger BOLD signals associated with viewing upright biological sequences, in fact, arise because of increased attention required to perform the 1-back task for those sequences. This argument can be rejected, however, because observers found this to be the easiest, least taxing of the three stimulus conditions. Moreover, their percent-correct performance was higher for the upright biological animations (73%) than for the inverted (58%) and the scrambled (48%) sequences which, according to observers, required more concentrated attention to perform. These reports are not surprising for the inverted and scrambled sequences, which lack the spatial structure that is so characteristic of biological motion animations. Keep in mind, too, that participants in this experiment were naive observers with no prior experience viewing point-light animations. The 1-back task proved challenging in all conditions, as evidenced by performance in even in the easiest condition — upright biological motion.

5. Experiment 2: visual and imagined biological motion

When asked to imagine a person engaged in some activity (e.g. throwing a ball), people experience no difficulty doing so. To what extent can imagination of biological activity modulate neural responses in posterior STS, the brain area so effectively activated upon actually viewing biological motion? For several reasons, we anticipated that imagination should be an effective 'stimulus' for STS activation. First, it is believed by many that imagination of an object or an event engages the same brain processes involved in perception of that actual object or event (e.g. Kosslyn, 1994). Consistent

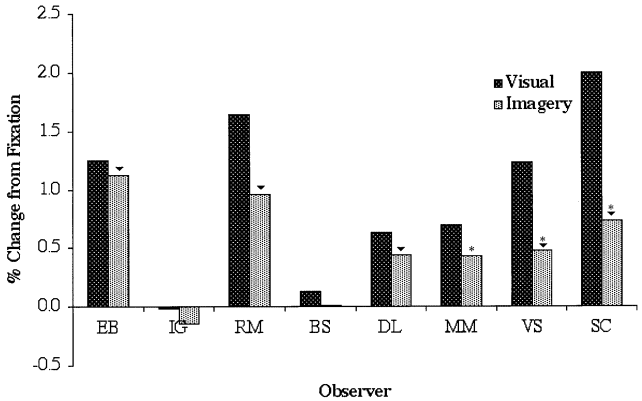

Fig. 4. Percent change of neural activity during passive viewing (dark bars) and mental imagery (light bars) of biological motion. BOLD signal is expressed as a percentage of the activity during passive fixation. (▼) Indicates statistically significant differences between the imagined biological motion condition and the fixation baseline. (∗) Indicates statistically significant differences between the viewing biological motion condition and the imagined biological motion conditions.

with this view are results from brain imaging studies showing that mental imagery can evoke activity in 'early' visual areas including V1, V2, and V3A (e.g. Kosslyn et al., 1999). Relevant for our purposes, mental imagery of motion patterns results in neural activity in area MT/MST, with the level of activation being approximately half that produced by real viewing of actual motion (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998). Encouraged by these earlier findings, we measured BOLD responses in posterior STS while observers imagined biological activities and compared those responses to activation levels when observers viewed actual animations of those activities.

5.1. Methods

Eight observers (four women, four men) participated in this experiment. All of these observers had participated in the localizer condition and so our analysis was confined to those regions on posterior STS that responded selectively to biological motion. Also, because these observers had participated in previous experiments involving biological motion, they were familiar with the point-light displays and were able to recall them for the imagery condition. Observers gave informed consent as approved by the Vanderbilt University Institutional Review Board.

This experiment consisted of three conditions interleaved within a single functional scan. Observers either passively viewed a fixation cross, passively viewed biological motion animations or imagined biological motion as depicted by the point-light animations. During the imagery condition, observers were prompted to imagine a given motion immediately following presentation of a verb in the center of the screen. The verbs always referred to biological activities seen during previous scans (e.g. walking, throwing, kicking), and they were presented at the same rate as the actual biological motion sequences (1-s presentation followed by a 1-s ISI). Observers did not perform any task other than imagery.

All analyses were conducted within the ROIs defined in the localizer condition. The 16-s stimulus phases were repeated periodically five times, resulting in 40 timepoints per stimulus condition. The volumes during which observers passively viewed the fixation cross were averaged into a single baseline activity level. Average activity levels for viewed and imagined biological motion are expressed as percent changes from the average fixation signal.

5.2. Results and discussion

Results are summarized in Fig. 4. In five out of eight of our observers, imagination of biological motion produced significantly stronger BOLD signals than did the fixation condition. For all observers, viewing biological motion resulted in stronger BOLD signals than did mental imagery (0.80 and 0.50%, respectively), the two conditions differing, on average, by a factor of two. Observers generally found the imagery condition to be somewhat difficult and to require greater mental concentration than the passive viewing condition. Nonetheless, this increased mental effort was not sufficient to boost the BOLD signal to the level produced by real motion. In other contexts, imagery is generally found to be weaker than perception (Kosslyn, 1994).

Is it possible that the act of imagining per se activates this region of the brain, regardless whether the imagined event is involved biological motion? To find out, we tested two new observers (one male, one female) on a modified imagery condition in which they imagined optic flow during one of the blocks in the scanning period. Immediately prior to this scanning session, these observers were shown actual optic flow sequences in which 500 dots moved radially inward and outward from a central fixation point at an average speed of approximately 6°/s. Both observers reported no difficulty imaging this stimulus during the imagery scanning session. The session itself consisted of three interleaved conditions: viewing real biological motion sequences, imagining biological motion, and imagining optic flow. Results from this series of measurements appear in Fig. 5. Again, viewing real biological motion sequences more strongly activated posterior STS than did imagining biological motion. However, mental imagery of biological motion produced stronger STS activation than did imagery of optic flow. This finding makes sense, because optic flow, coherent motion and

kinetic motion boundaries are ineffective stimuli for activating STS (Grossman et al., 2000).

In these two observers we also examined BOLD signals arising within the MT/MST complex, a brain region located more ventral and medial to area STS. Recall that Kourtzi and Kanwisher (2000) found activation in the MT/MST complex when observers viewed static pictures of individuals engaged in activity, but not when observers viewed pictures of people at rest. We used real optic flow to localize voxels corresponding to the MT/MST complex (whose anatomical location in the human brain is no longer in question), and then measured activation levels within those voxels associated with imagining biological motion and imagining optic flow. Both imagery conditions produced activation above baseline in MT/MST, although neither imagery condition produced activation as large as that associated with viewing real motion. It is not surprising that both forms of imagined motion activate MT/MST, for our earlier work showed that this area responds to both coherent motion and biological motion. Somewhat surprisingly, imagined biological motion produced higher MT/MST activation than did imagined optic flow in one observer. Recall, however, that the 'biological' imagery condition was judged to be demanding by our participants, including this observer.

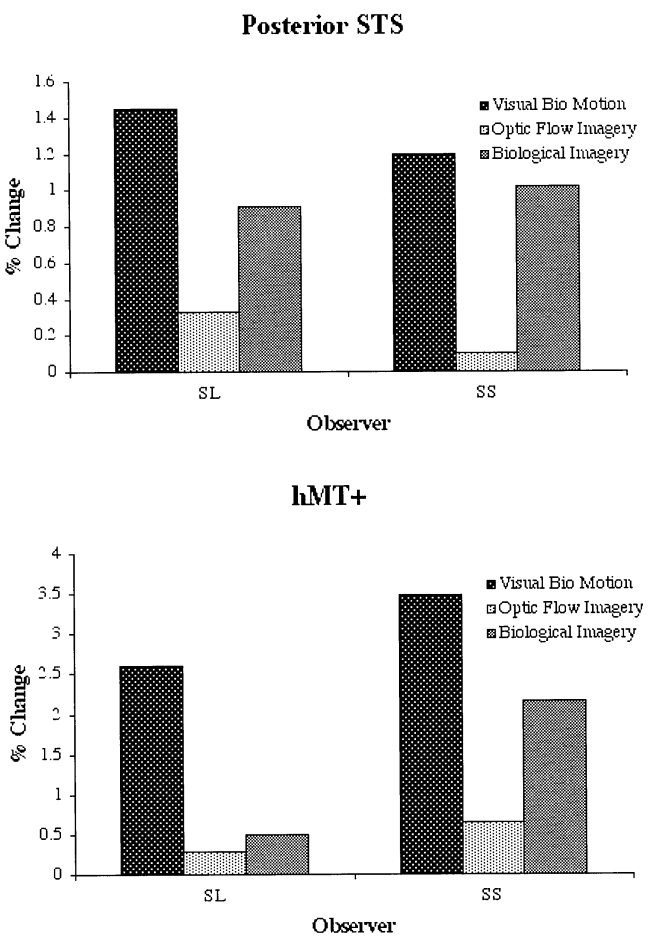

Fig. 5. Neural response of posterior STS and MT/MST from two observers during viewing biological motion (black bars), imagining biological motion (light gray bars), and optic flow imagery (dark gray bars). Activity level is expressed as percent change in neural activity associated with biological motion viewing and imagery relative to optic flow imagery baseline.

6. Conclusion

The present results add further evidence to the notion that the human brain contains neural machinery, including area STS, specialized for registering the unique motion vectors associated with animate activity. Those vectors comprise a set of hierarchical pendular motions which, when displayed with appropriate temporal phases, create the special form of structure from motion termed biological motion (Cutting, 1981; Webb & Aggarwal, 1982; Pinto & Shiffrar, 1999). While not a full parametric study of biological motion, the present experiments show that the level of activity within STS, as indexed by the BOLD response, is correlated with the salience of the displays evoking that activity.

Our findings also provide another piece of evidence implicating common brain areas in perception and imagery (e.g. Kosslyn et al., 1999), in this case perception and imagination of biological activity. Our imagery results also suggest an interpretation for the activations in MT/MST measured by Kourtzi and Kanwisher (2000) when observers viewed static pictures of people engaged in activity. We suggest that those activations may have been mediated by peoples' imagining the activity implied in the still pictures, an idea consonant with Kourtzi and Kanwisher's appeal to 'top down' influences.

Much still remains to be learned about STS's involvement in perception of biological motion. Is STS activation limited to human motion, or will animations depicting animal motion activate this region as well? Is whole-body activity necessary, or will STS respond to movement of body parts? In this regard, it is interesting to note that Puce, Allison, Bentin, Gore, & McCarthy (1998) found activation along the STS in response to eye and mouth movements. It has also been reported that STS responds more to speech sounds than to non-vocal environmental sounds (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000). It will be interesting to learn whether STS activity can also be evoked by sounds associated with other biological activities, such as running or clapping.

Acknowledgements

Supported by grants from NIH (EY07135), the Defense University Research Initiative Program, and the Vanderbilt University Discovery Program.

References

Ahlström, V., Blake, R., & Ahlström, U. (1997). Perception of biological motion. *Perception*, *26*, 1539–1548.

Belin, P., Zatorre, R. J., Lafaille, P., Ahad, P., & Pike, B. (2000). Voice-selective areas in human auditory cortex. *Nature*, *403*, 309–312.

Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *Journal of Neuroscience*, *16*, 3737–3744.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 443–446.

Cheng, K., Fujita, H., Kanno, I., Miura, S., & Tanaka, K. (1995). Human cortical regions activated by wide-field visual motion: an H215O PET study. *Journal of Neurophysiology*, *74*, 413–427.

Cowey, A., & Vaina, L. M. (2000). Blindness to form from motion despite intact static form perception and motion detection. *Neuropsychologia*, *38*, 566–578.

Cox, R. W., & Hyde, J. S. (1997). Software tools for analysis and visualization of FMRI data. *NMR in Biomedicine*, *10*, 171–178.

Cutting, J. (1981). Coding theory adapted to gait perception. *Journal of Experimental Psychology: Human Perception & Performance*, *7*, 71–87.

Dupont, P., Orban, G. A., De Bruyn, B., Verbruggen, A., & Mortelmans, L. (1994). Many areas in the human brain respond to visual motion. *Journal of Neurophysiology*, *72*, 1420–1424.

Goebel, R., Khorram-Sefat, D., Muckli, L., Hacker, H., & Singer, W. (1998). The constructive nature of vision: direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. *European Journal of Neuroscience*, *10*, 1563–1573.

Grossman, E. D., Donnelly, M., Price, P., Morgan, V., Pickens, D., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience*, *12*(5), 711–720.

Howard, R. J., Brammer, M., Wright, I., Woodruff, P. W., Bullmore, E. T., & Zeki, S. (1996). A direct demonstration of functional specialization within motion-related visual and auditory cortex of the human brain. *Current Biology*, *6*, 1015–1019.

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception and Psychophysics*, *14*, 201–211.

Kosslyn, S. M. (1994). *Image and mind*. Cambridge, MA: Harvard University Press.

Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J. P., Thompson, W. L., Ganis, G., Sukel, I. E., & Alpert, N. M. (1999). The role of area 17 in visual imagery: convergent evidence from PET and rTMS. *Science*, *284*, 167–170.

Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, *12*, 48–55.

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., & Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in the human occipital cortex. *Proceedings of the National Academy of Sciences USA*, *92*, 8135–8139.

Orban, G. A., Dupont, P., De Bruyn, B., Vogels, R., Vandenberghe, R., & Mortelmans, L. (1995). A motion area in human visual cortex. *Proceedings of the National Academy of Sciences USA*, *92*, 993–997.

Pavlova, M., & Sokolov, A. (2000). Orientation specificity in biological motion perception. *Perception & Psychophysics*, *62*, 889–898.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.

Pinto, J., & Shiffrar, M. (1999). Subconfigurations of the human form in the perception of biological motion displays. *Acta Psychologica*, *102*, 293–318.

Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Cognitive Neuroscience*, *6*, 99–116.

Rees, G., Friston, K., & Koch, C. (2000). A direct quantitative relationship between the functional properties of human and macaque V5. *Nature Neuroscience*, *3*, 716–723.

Schenk, T., & Zihl, J. (1997a). Visual motion perception after brain damage: I. Deficits in global motion perception. *Neuropsychologia*, *35*, 1289–1297.

Schenk, T., & Zihl, J. (1997b). Visual motion perception after brain damage: II. Deficits in form-from-motion perception. *Neuropsychologia*, *35*, 1299–1310.

Sumi, S. (1984). Upside down presentation of the Johannson moving light spot pattern. *Perception*, *13*, 283–286.

Sunaert, S., Van Hecke, P., Marchal, G., & Orban, G. A. (1999). Motion-responsive regions of the human brain. *Experimental Brain Research*, *127*, 355–370.

Tootell, R. B. H., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., Rosen, B. R., & Belliveau, J. W. (1995). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *The Journal of Neuroscience*, *15*, 3215–3230.

Vaina, L. M., Lemay, M., Bienfang, D. C., Choi, A. Y., & Nakayama, K. (1990). Intact 'biological motion' and 'structure from motion' perception in a patient with impaired motion mechanisms: A case study. *Visual Neuroscience*, *5*, 353–369.

Van Oostende, S., Sunaert, S., Van Hecke, P., Marchal, G., & Orban, G. A. (1997). The kinetic occipital (KO) region in man: An fMRI study. *Cerebral Cortex*, *7*, 690–701.

Watanabe, T., Harner, A. M., Miyauchi, S., Saski, Y., Nielsen, M., Palomo, D., & Mukai, I. (1998). Task-dependent influences of attention on the activation of human primary visual cortex. *Proceedings of the National Academy of Sciences*, *95*, 11489–11492.

Watson, J. D. G., Myers, R., Frackowiak, R. S. J., Hajnal, J. V., Woods, R. P., Mazziotta, J. C., Shipp, S., & Zeki, S. (1993). Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cerebral Cortex*, *3*, 79–94.

Webb, J. A., & Aggarwal, J. K. (1982). Structure from motion of rigid and jointed objects. *Artificial Intelligence*, *19*, 107–130.