The Neural Substrates of Biological Motion Perception: an fMRI Study

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We used fMRI to identify the brain areas related to the perception of biological motion (4 T EPI; whole brain). In experiment 1, 10 subjects viewed biological motion (a human figure jumping up and down, composed of 21 dots), alternating with a control stimulus created by applying autoregressive models to the biological motion stimulus (such that the dots' speeds and amplitudes were preserved whereas their linking structure was not). The lengths of the stimulus bouts varied, and therefore the transitions between biological motion and control stimuli were unpredictable. Subjects had to indicate with a button press when each transition occurred. In a related biological motion task, subjects detected short (1 s) disturbances within these displays. We also examined the neural substrates of motion and shape perception, as well as motor imagery, to determine whether or not the cortical regions involved in these processes are also recruited during biological motion perception. Subjects viewed linear motion displays alternating with static dots and a series of common objects alternating with band-limited white noise patterns. Subjects also generated imagery of their own arm movements alternating with visual imagery of common objects. Biological motion specific BOLD signal was found within regions of the lingual gyrus at the cuneus border, showing little overlap with object recognition, linear motion or motion imagery areas. The lingual gyrus activation was replicated in a second experiment that also mapped retinotopic visual areas in three subjects. The results suggest that a region of the lingual gyrus within VP is involved in higher-order processing of motion information.

Introduction

Humans are very good at perceiving the movements performed by others. They can readily recognize an actor's movements even from a display consisting only of the motion of point lights corresponding to the joints of the actor – this has been termed 'biological motion' (Johansson, 1973). Each individual static frame looks like a meaningless scatter of dots, but once the frames are animated, observers immediately perceive the action performed by the actor. In addition, with the same limited information people can make more specific categorizations such as male or female, friend or stranger (Cutting and Kozlowski, 1977; Mather and West, 1993). Behavioral studies also suggest the existence of highly sensitive and flexible mechanisms for the analysis of biological motion (Neri *et al*., 1998). However, the specific neural substrate for the analysis of biological motion is still an unanswered question.

Oram and Perrett reported neurons in the anterior section of the superior temporal polysensory area (STPa) in the monkey that responded selectively to such biological motion (Oram and Perrett, 1994). It has been suggested that processing of visual information in primates follows two pathways: the ventral 'form', or 'what', pathway and the dorsal 'motion', or 'where/how', pathway (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992). Area STPa receives inputs from both the ventral and dorsal pathways (Felleman and Van Essen, 1991). Thus, it has been suggested that outputs from the dorsal pathway (e.g. areas MT and MST) which deal with motion information, and outputs from the ventral pathway (e.g. area IT) which deal with form information, are integrated in the STPa cells and contribute to the perception of biological motion. Several human neuroimaging studies have reported activation in the posterior superior temporal sulcus/superior temporal gyrus (STS/STG; a region possibly encompassing the human homologue of area STPa) during the observation of biological motion (Bonda *et al*., 1996; Howard *et al*., 1996).

Human neuropsychological research suggests that a separate site from STPa is involved in biological motion perception. Patient AF with damage to occipitoparietal cortex and patient LM with damage to dorsal occipitotemporal cortex both show specific deficits in many early aspects of motion analysis but normal biological motion processing (Vaina *et al*., 1990; McLeod *et al*., 1996). Presumably, area MT and associated motion-processing areas were damaged in these two patients; thus, inputs from the dorsal motion pathway to the human homologue of area STPa would no longer exist in these two patients. This evidence suggests the existence of a separate motion pathway, specialized for the perception of biological motion, that may not require processing within the STS. In contrast to these two patients, patient AL cannot recognize form-from-motion, although she performs like normals on low-level motion tasks. That is, AL can detect speed differences and the direction of motion, but is impaired at recognizing two- or three-dimensional form generated by motion (including Johansson figures). Damage to the fusiform and lingual gyri that extends to latero-ventral areas of the temporal lobe are most likely the source of AL's perceptual inabilities (Cowey and Vaina, 2000). Based on these patient findings, the ventral pathway and not the dorsal pathway appears critical for form-from-motion perception.

Consistent with this neuropsychological evidence, Zeki has proposed that area V3 is a dynamic-form area on the basis of neural connections within the occipital lobe (Zeki, 1993). Motion information projects to MT from V1 and V2 and then re-enters these visual areas diffusely, including areas which project to V3; an area that contains form-sensitive neurons. Additionally, the magnocellular layers of V1 and V2 project directly to V3. Thus, both the direct and re-entry connections provide a mechanism for form and motion to be integrated in V3, making it a likely site in generating form-from-motion. Interestingly, previous neuroimaging studies have placed little emphasis on the role of V3 in the computation of biological motion. For example, Howard *et al*. (Howard *et al*., 1996) observed activation in V3 and Bonda *et al*. (Bonda *et al*., 1996) found activation within prestriate cortex which likely included V3, however these observations were overshadowed by the STS activation also observed in these studies.

The suggestion that two separate regions mediate biological

motion perception parallel findings from face perception research. Face-sensitive neurons are found not only in monkey IT (Gross *et al.*, 1972) and in human ventral occipitotemporal cortex (fusiform face area) (Kanwisher *et al.*, 1997) but also in monkey and human STS (Perrett *et al.*, 1991; Puce *et al.*, 1998). Monkey IT and human fusiform gyrus are sensitive to the invariant aspects of faces that are required for face identification (Hasselmo *et al.*, 1989; Hoffman and Haxby, 2000). In contrast, human and monkey STS tend to respond to variant aspects of the face (e.g. gaze and mouth movements) that communicate social intentions or meaning (Perrett *et al.*, 1991; Puce *et al.*, 1998; Hoffman and Haxby, 2000). Given that such biological stimuli as faces may be processed by more than one region, it is possible that the perception of biological motion is also subserved by multiple regions.

Consensus has not yet been reached about which brain regions are critical for biological motion perception. Using fMRI, Howard *et al.* found bilateral activation both in the MT/MST complex and in the STG anterior to it during the observation of biological motion compared with random motion (Howard *et al.*, 1996). On the other hand, Bonda *et al.* found activation mainly in the right STS and limbic structures such as the amygdala, but did not find activation in MT/MST (Bonda *et al.*, 1996). One reason for these discrepancies might be the difficulty of generating good control stimuli which have local motion characteristics highly similar to biological motion but lack global structure. However, a recent fMRI study has succeeded at creating such perceptually appropriate controls (Grossman *et al.*, 2000). In this study, biological motion was found to activate primarily the posterior STS and also somewhat area MT. A further strength of this study was their use of an active task (one-back task) throughout the experiment. Although the STS region located by Grossman *et al.* (Grossman *et al.*, 2000) and Bonda *et al.* (Bonda *et al.*, 1996) are fairly similar, Howard *et al.* (Howard *et al.*, 1996) located a more superior, anterior, and medial region compared to the regions located by these other two studies. Therefore, there is still ambiguity surrounding the specific locale within the STS/STG that is involved in biological motion perception. Moreover, it is unclear whether regions in addition to the STS are also involved in biological motion.

Another question of interest is whether the mechanisms responsible for the perception of biological motion overlap with those involved in motor execution and/or motor imagery. Motor imagery has been shown to activate many areas involved in motor execution, such as supplementary motor area, superior premotor cortex, inferior premotor cortex (Brodmann's areas 44/45), superior and inferior parietal regions and cerebellum (Parsons *et al.*, 1995). In addition, a PET study has revealed that the observation of meaningful action also activates inferior premotor cortex (Grèzes *et al.*, 1998). Apparent motion of human movements is also found to activate motor and parietal cortex in humans (Stevens *et al.*, 2000). In contrast, Bonda *et al.* (Bonda *et al.*, 1996) did not find activation in motor-related areas during observation of whole-body point-light movements, although they found activation in parietal cortex during observation of point-light hand movements.

In the present fMRI study, we investigated the cortical activation patterns of subjects observing biological motion in comparison with control stimuli. We also used three control tasks to determine if the cortical region(s) sensitive to biological motion can be dissociated from regions involved in linear motion perception, object perception, and motor imagery.

Experiment I

Materials and Methods

Subjects

Ten neurologically intact adult volunteers (five males and seven females, mean age 25 years) participated in the study. Informed consent was obtained from all the subjects prior to the experiment. The protocol of the present study was in accordance with the ethical guidelines of the Robarts Research Institute (London, ON, Canada).

General Procedure

Subjects participated in five functional runs two of which consisted of biological motion stimuli and three of which consisted of linear motion stimuli, object perception stimuli, and motor imagery. Each functional run lasted 360 s and consisted of six 60 s stimulus–control cycles. All stimuli were presented in MATLAB, using the extensions provided by the high-level Psychophysics Toolbox (Brainard, 1997) and low-level Video Toolbox (Pelli, 1997). In the biological motion, linear motion and object perception experiments, subjects were instructed to fixate in the center of the stimulus display.

Generation of Biological Motion Stimuli and Control Stimuli

Point-light displays of biological motion stimuli were generated by recording sequences of whole-body jumping movements, using the Optotrak, an optoelectronic imaging system. Twenty-one light-points were attached to major joints of the body (head, neck, torso, and both shoulders, elbows, wrists, hands, hips, knees, ankles, heels, and toes). The control stimuli were created by applying autoregressive models to the biological motion stimuli using TIMSAC (Akaike *et al.*, 1979; Kitagawa and Akaike, 1981) such that the dots' positions, speeds and amplitudes were preserved whereas their linking structure was not. First, three-dimensional joint position data acquired by the Optotrak were projected onto a plane. A univariate autoregressive (AR) model was applied separately to the x and y coordinates of each joint position's 8 s data set sampled at 60 Hz. Coefficients of each AR model and covariance of innovation (system noise input) were estimated using the least square error method (UNIVAR program in TIMSAC). The order of the AR models ranged from 3 to 50. Control stimuli were then produced by applying artificially generated Gaussian white noise as input to the noise component of each model. Both stimuli were centered in the display and occupied a 8.0° by 8.0° area.

Figure 1 shows a portion of the biological motion and control stimulus sequences presented to the subjects. Figure 2 shows mean position, amplitude and velocity of each joint, and mean rate of change of the link length between each pair of joints. Larger changes in the relative positions of joints in the control stimuli, compared to those in the biological motion stimuli, suggest that the linking structures were destroyed. However, little overall difference in the properties of individual joints suggests similar basic attributes for the two types of stimuli. Figure 3 shows examples of position–velocity plots for individual joints in the x- and y-planes. The overlap between the dashed and solid curves found in each panel also suggests the similarity in basic attributes of the two types of stimuli. By sequentially adding biological motion stimuli and control stimuli with a smoothly changing weight, smooth transitions between biological motion stimuli and control stimuli were generated for the first biological motion task. Using the procedure that was used to generate the control stimuli, small disturbances were inserted during biological motion and control stimuli for the second biological motion task (1 s random motions for biological motion stimuli, and 1 s sinusoidal motions for control stimuli).

The Tasks

Biological Motion Perception with Detection of Gradual Transitions. Because the lengths of the stimulus bouts varied (20, 25, 30, 35 or 40 s), the transitions between biological motion and control stimuli were unpredictable. Subjects had to indicate the transitions with a right button press.

Biological Motion Perception with Detection of Disturbances. Stimulus bouts of constant length were used. During presentation of

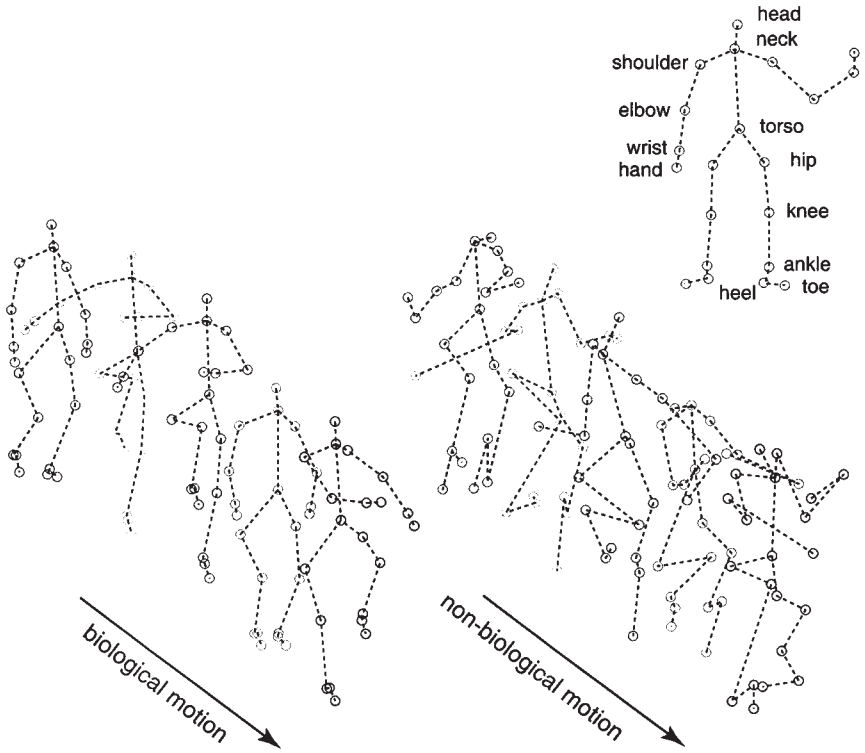

Figure 1. Example segments of the biological motion and control motion sequences presented to the subjects. Note that dashed lines connecting joints (links) were not visible to the subjects. Only the joints indicated by circles were shown (white dots on a black background).

biological or control stimuli, subjects had to detect (with a right button press) short (1 s) disturbances within the biological or control stimuli. Each bout had zero, one or two disturbances.

Linear Motion Perception. Subjects observed 200 randomly moving dots (mean velocity of 4°/s). As control stimuli, individual frames randomly selected from the linear motion sequence were presented for 500 ms and alternated with 500 ms presentations of a blank screen with the same mean luminance. The stimuli subtended 12.6° by 12.6°.

Common Object Perception. Subjects observed images of common objects alternating with band-limited white noise patterns (Fig. 4*A*). Each image was presented for 2 s, and subjects passively observed the images. The stimuli subtended 6.4° by 5.6°.

Motor Imagery. Subjects were asked to generate imagery of their arm(s) performing various tasks alternating with a visual imagery task requiring size judgements. During the motor imagery period, sentences such as 'scratch back with left hand' were presented (Fig. 4*B*). During the visual imagery period, sentences such as 'which larger: airplane or truck' were presented. Each sentence were presented for 2 s, followed by a 4 s gray screen during which subjects generated imagery.

MRI Acquisition

Images were collected with a 4.0 T, whole-body MRI system (Varian, Palo Alto, CA; Siemens, Erlangen, Germany) at the Robarts Research Institute (London, ON, Canada), using a quadrature head coil. The field of view was 20.0 × 20.0 × 14.4 cm, with an in-plane matrix of 64 × 64 pixels and 24 contiguous axial slices, resulting in a voxel size of 3.125 × 3.125 × 6 mm. Each volume (24 slices) was sampled once every 5 s. Slices were obtained to encompass the entire cerebral cortex and the upper half of cerebellum. Functional data were collected using T_2*-weighted segmented gradient echo-planar imaging (T_E = 15 ms, T_R = 1.2338 s, four shots, flip angle = 60°, navigator-corrected) for BOLD-based imaging. Functional activation data were superimposed onto high-resolution T_1-weighted anatomical images.

MRI Analysis

All functional images were temporally filtered by a low-pass Gaussian filter (FWHM = 2). Time courses within each voxel (72 time points) were corrected for linear drift. All functional imaging data were preprocessed and analyzed using Brain Voyager 3.9. Correlation maps were generated for each subject by cross-correlating the BOLD response for a given task with a reference time course corresponding to the conditions within that task. Reference time courses were corrected according to the hemodynamic response function. Individual high-resolution volume anatomies (0.75 × 0.75 × 1.5 mm) were transformed into the Talairach coordinate system (Talairach and Tournoux, 1988). The resulting transformation was applied to the functional volumes. Finally, a general linear model multi-subject analysis (non-separate predictor for each subject) was performed for each of the five experiments to generate group-average maps.

Results

Biological Motion Perception

Figure 5*A* shows the regions activated at the $P < 0.001$ (all P values uncorrected) level of significance by the two biological motion tasks, overlaid on the anatomical image of one subject (which has been transformed into the Talairach coordinate system). Significant activation was found only in the lingual gyrus at the cuneus border (see Table 1). The high degree of overlap between the regions responsive to the two biological motion tasks indicates the reliability of the contribution of these areas to biological motion perception. Although the group analyses did not demonstrate significant activation in the STG, individual analyses showed that five subjects displayed STG activation in the biological motion experiment involving gradual transitions ($P < 0.001$) and three subjects showed STG activation in the biological motion with disturbances experiment ($P <$

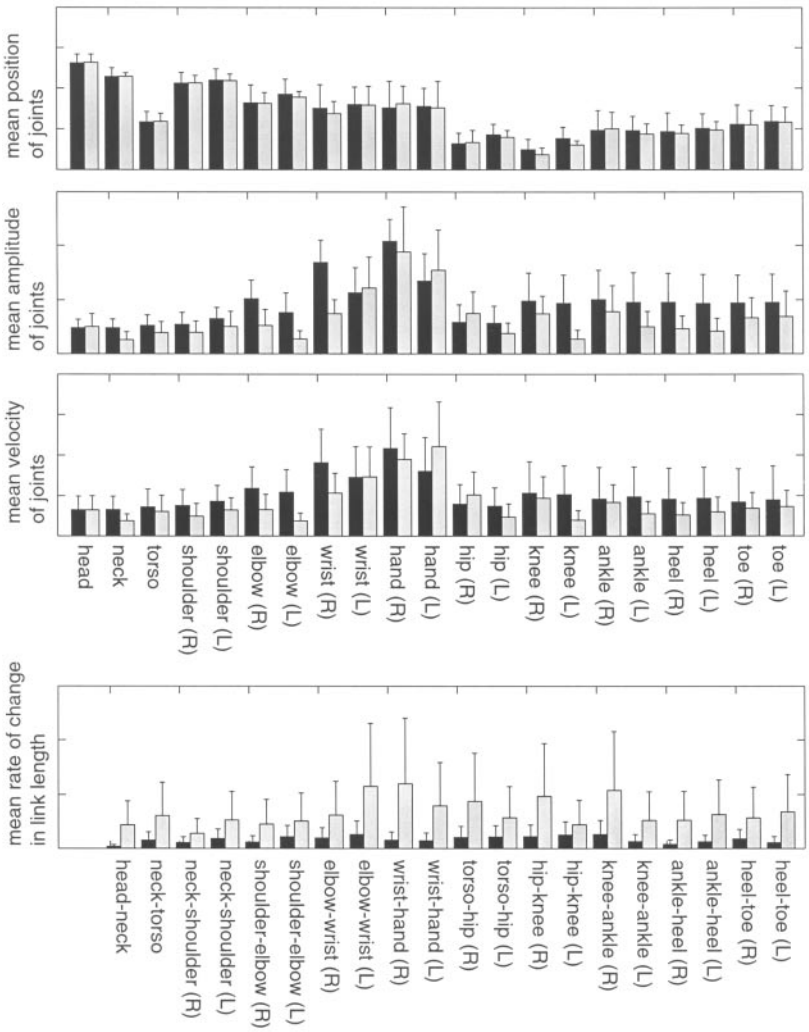

Figure 2. Properties of biological and non-biological motion stimuli. Mean position, amplitude, and velocity of each joint, and mean rate of change of the link length between each pair of joints are shown. Black bars denote biological motion stimuli and gray bars denote control stimuli generated with an autoregressive model. Error bars show SD.

0.001). Group analyses revealed no significant activation in MT/MST.

During both active tasks, performance was more than 90% accurate for both biological motion and control sequences, indicating that subjects were attending to the stimuli.

Linear Motion Perception

Figure 5*B* shows the regions activated by linear motion perception in comparison to static dots ($P < 0.00001$). As many others have found (Zeki *et al.*, 1991; Watson *et al.*, 1993; Dupont *et al.*, 1994; Tootell *et al.*, 1995; Rees *et al.*, 2000), we found bilateral activation in lateral temporal–occipital–parietal cortex (the human homologue of MT/MST, see Table 1).

Common Object Perception

Figure 5*C* shows the regions activated by object perception in comparison to white noise patterns ($P < 0.00001$). Bilateral activations were found in the fusiform gyrus (see Table 1), consistent with previous work showing activation in this region during object and face perception (Kanwisher *et al.*, 1996, 1997).

Motor Imagery

Figure 5*D* shows the regions activated by motor imagery in comparison to visual object imagery ($P < 0.0001$). Activations were found in the left precentral gyrus and the left inferior parietal lobe (see Table 1), both of which are involved in motor execution (see Table 1). In our motor imagery task, 19 commands out of 30 involved right-hand movements, while seven involved the left hand, and four involved both hands. Therefore, it is reasonable that we found higher left-hemisphere activation in this task.

Overlap Between Biological Motion Perception and the Other Tasks

We did not find overlap between the areas sensitive to biological motion and the areas involved in the perception of motion and shape, or the generation of motor imagery. This conclusion held even when we lowered the significance levels of these three tasks to that used for the biological motion tasks (i.e. $P < 0.001$).

Discussion

Our results show that the biological motion stimuli activated the lingual gyrus at the cuneus border, whereas previous neuroimaging studies have reported the involvement of inferior, middle and superior temporal regions as well as parietal and lateral occipital regions. On the other hand, our finding complements observations in patient AL (Cowey and Vaina, 2000). As

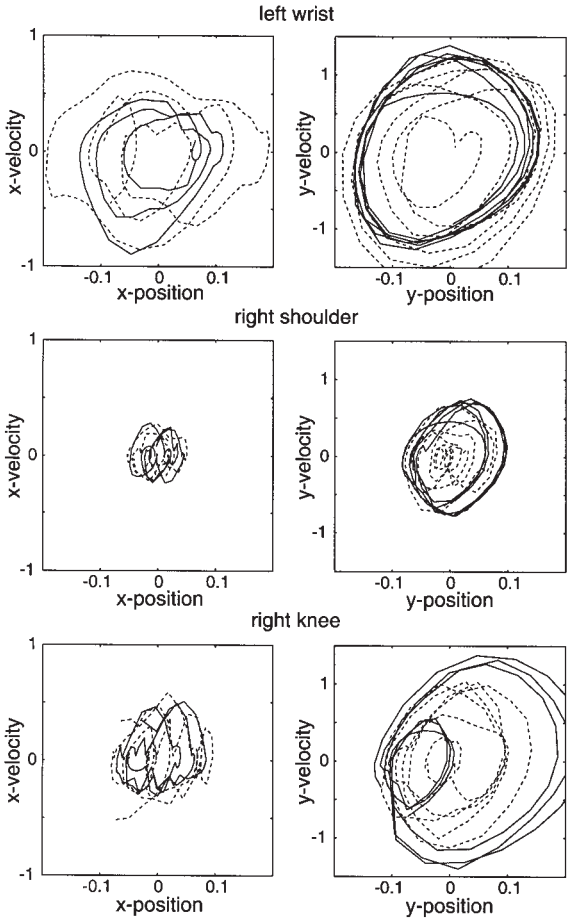

Figure 3. Examples of position–velocity plots of joints. Examples of position–velocity plots of individual joints in the *x*- and *y*-planes (left wrist, right shoulder and right knee). Solid curves indicate biological motion stimuli. Dashed curves indicate control stimuli. Values are normalized such that the maximum height of the stimuli is 1.

discussed in the Introduction, AL is impaired at recognizing form-from-motion as a result of a lesion in the lingual and fusiform gyri. Although AL's perceptual inabilities could be due to lingual gyrus inputs to biological motion specific regions being disconnected, the present finding provides evidence that the lingual gyrus directly mediates biological motion perception.

Human neuroanatomical work suggests that the lower parts of the second (V2) and third (VP – the ventral component of V3) visual areas lie on the lingual gyrus, whereas the analogue of the macaque's fourth visual area probably lies on the fusiform gyrus (Clarke and Miklossy, 1990). It is possible that the region we found lies within VP. Thus, our finding may provide support for Zeki's hypothesis concerning the role of V3 in form-from-motion perception (Zeki, 1993). To determine whether the area lies within VP, we conducted a second experiment that mapped retinotopic visual areas. An additional purpose of the second experiment was to replicate our biological motion finding, given that few studies have detected activation within the lingual gyrus.

Experiment 2

Materials and Methods

Subjects

Three neurologically intact adult volunteers (one male and two females, mean age 25 years) participated in the experiment. Informed consent was obtained from all the subjects prior to the experiment. The protocol of the present study was in accordance with the ethical guidelines of the Robarts Research Institute (London, ON, Canada).

Table 1
Activation foci in each condition of experiment 1

Condition	Brain region	Brodmann's area	Talairach coordinates		
			x	*y*	*z*
Biological motion	R lingual gyrus	30/18/19	5	–68	8
	Cuneus	18	0	–80	8
Linear motion	L middle temporal gyrus	37	–41	–69	0
	R middle temporal gyrus	37	41	–68	1
Common objects	L fusiform gyrus	37	–32	–43	–17
	R fusiform gyrus	37	30	–44	–18
Motor imagery	L precentral gyrus	6	–28	–11	55
	L inferior parietal lobe	40	–38	–49	55

General Procedure

Subjects participated in two functional runs. One run consisted of biological motion stimuli and the other run consisted of polar angle stimuli. The biological motion and polar angle runs lasted 360 s (six 60 s stimulus–control cycles) and 288 s (six 48 s periods), respectively. In both runs, subjects were instructed to fixate in the center of the stimulus display.

The Tasks

Biological Motion Perception with Detection of Disturbances. See experiment 1 methods.

Polar Angle Perception. Subjects fixated while a contrast-reversing (8 Hz) 45° black and white checkerboard wedge, presented on a uniform gray field, rotated 360° about the fixation point. The viewing aperture was 14.25°. This method is similar to previous retinotopic mapping studies of visual cortex (Sereno *et al*., 1995; Engel *et al*., 1997).

MRI Acquisition

Images were collected with a 4.0 T, whole-body MRI system (Varian, Palo Alto, CA; Siemens, Erlangen, Germany) at the Robarts Research Institute (London, ON, Canada), using a quadrature head coil. Functional data were collected using T_2^*-weighted segmented gradient echo-planar imaging. In the biological motion run, the field of view was 19.2 × 19.2 × 6.60 cm, with an in-plane matrix of 64 × 64 pixels and 11 pseudo-coronal slices, resulting in a voxel size of 3.0 × 3.0 × 6.0 mm (T_E = 15 ms, T_R = 750 ms, two shots, flip angle = 40°, navigator-corrected). In the polar angle run, the field of view was 19.2 × 19.2 × 5.5 cm, with an in-plane matrix of 128 × 128 pixels and 11 pseudo-coronal slices, resulting in a voxel size of 1.5 × 1.5 × 5.0 mm (T_E = 15 ms, T_R = 1000 ms, four shots, flip angle = 40°, navigator-corrected). The anatomies were sampled pseudo-coronally in a 19.2 × 19.2 × 25.6 cm field of view at high resolution (voxel size: 0.75 × 0.75 × 1.00 mm).

MRI Analysis

The biological motion data were analyzed in the same way as in experiment 1 (see experiment 1 methods), except that the GLM analysis was conducted separately for each subject. Given that most biological motion activation was medial with a slight right hemisphere bias, retinotopic analysis was restricted to the right hemisphere.

The polar angle data were first processed to remove any slow drift trends and then cross-correlated with six phase delays to a reference function of 6, 48 s cycles (4 s on; 44 s off). Each voxel was colored according to the lag value with which it correlated highest. By identifying patterns of phase reversals in the activation displayed on the flattened maps, the retinotopic visual areas (V1, V2, V3 and VP) were determined for each subject. This technique of delineating visual area borders is similar to previous studies [e.g. (Sereno *et al*., 1995; Engel *et al*., 1997)].

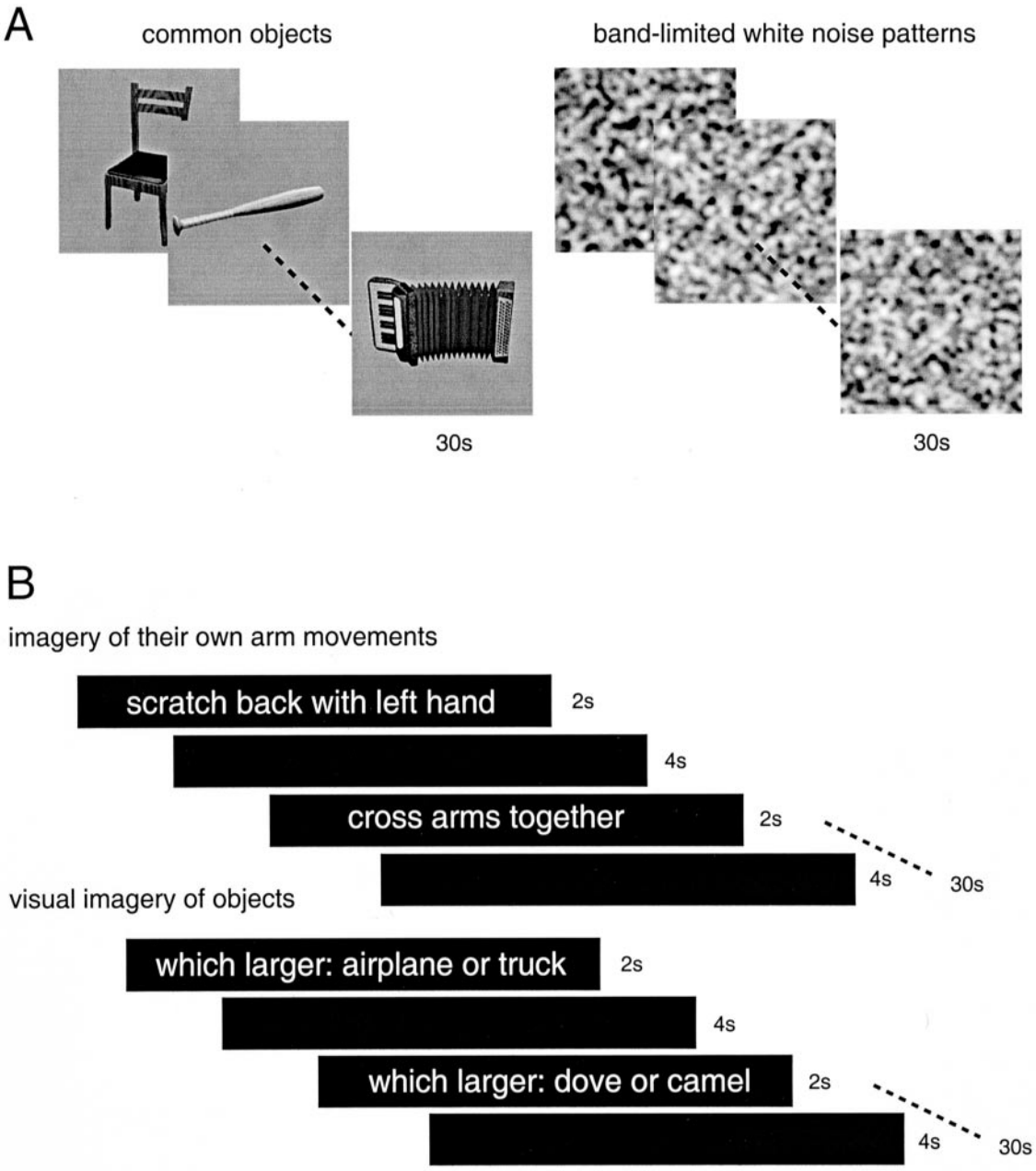

Figure 4. Common objects stimuli and motion imagery stimuli. (*A*) Examples of common objects (left) and band-limited white noise patterns used as control stimuli (right). (*B*) Examples of motor and visual imagery sentences.

The biological motion data were overlaid onto each subject's flattened map and the visual area borders were then overlaid.

In addition to transforming the high-resolution volume anatomies to the Talairach coordinate system (as in experiment 1), the cortical surfaces were rendered, inflated, and flattened. In isolating the cortical surface, first the skull and subcortical structures were stripped off, and the ventricles filled. The gray–white matter boundary was determined by a region growing technique and dilated to a point within gray matter (approximately beneath layer 4). After smoothing the border, the hemispheres were disconnected and any handles or topological errors were removed through an automated algorithm (Kriegeskorte and Goebel, 2001). The resulting border for each hemisphere was used to create a three-dimensional reconstruction of the cortical sheet, which was inflated and then cut in five places. The surface was unfolded outwards from the cuts. A similar unfolding technique has been reported previously (Goebel *et al*., 1998).

Results

Figure 6 shows, for each subject, the activation produced by the biological motion task ($P < 0.000001$) projected onto a flattened cortical representation with visual area borders overlaid. The results replicate the lingual gyrus finding of experiment 1. Voxels with the highest correlation values are located within VP (two subjects) or at the VP/V2 border (one subject).

As in experiment 1, during the biological motion task, performance was more than 90% accurate for both biological motion and control sequences, indicating that subjects were attending to the stimuli.

Discussion

The experiment 2 results replicate those of experiment 1 — a

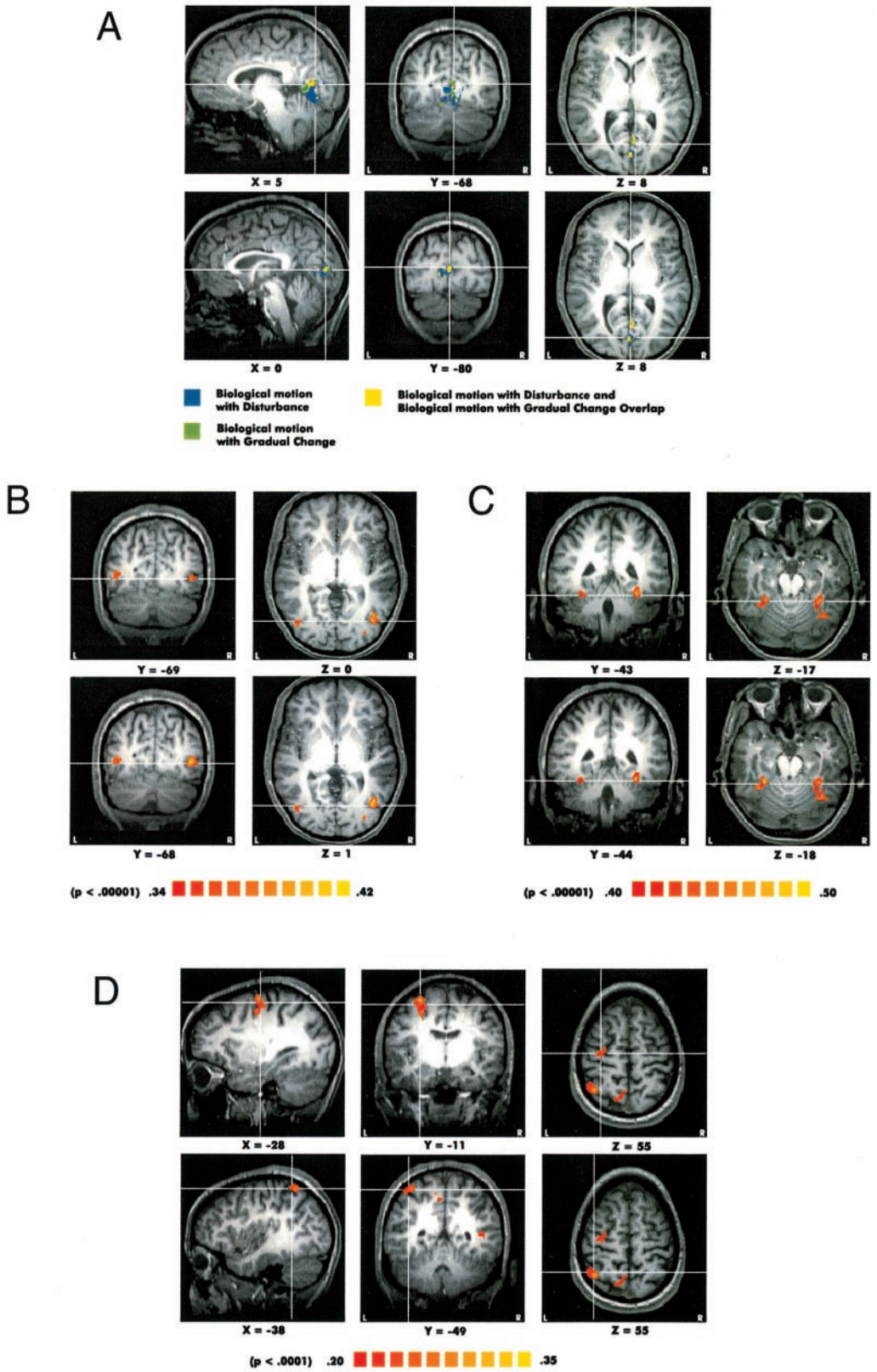

Figure 5. Average activation map for each task. The results of group analysis were overlaid on the anatomical image of one subject transformed into the Talairach coordinate system. (*A*) The regions activated by the two biological motion tasks. (*B*) The regions activated by linear motion perception in comparison to static dots. (*C*) The regions activated by common object perception in comparison to white noise patterns. (*D*) The regions activated by motor imagery in comparison to visual imagery.

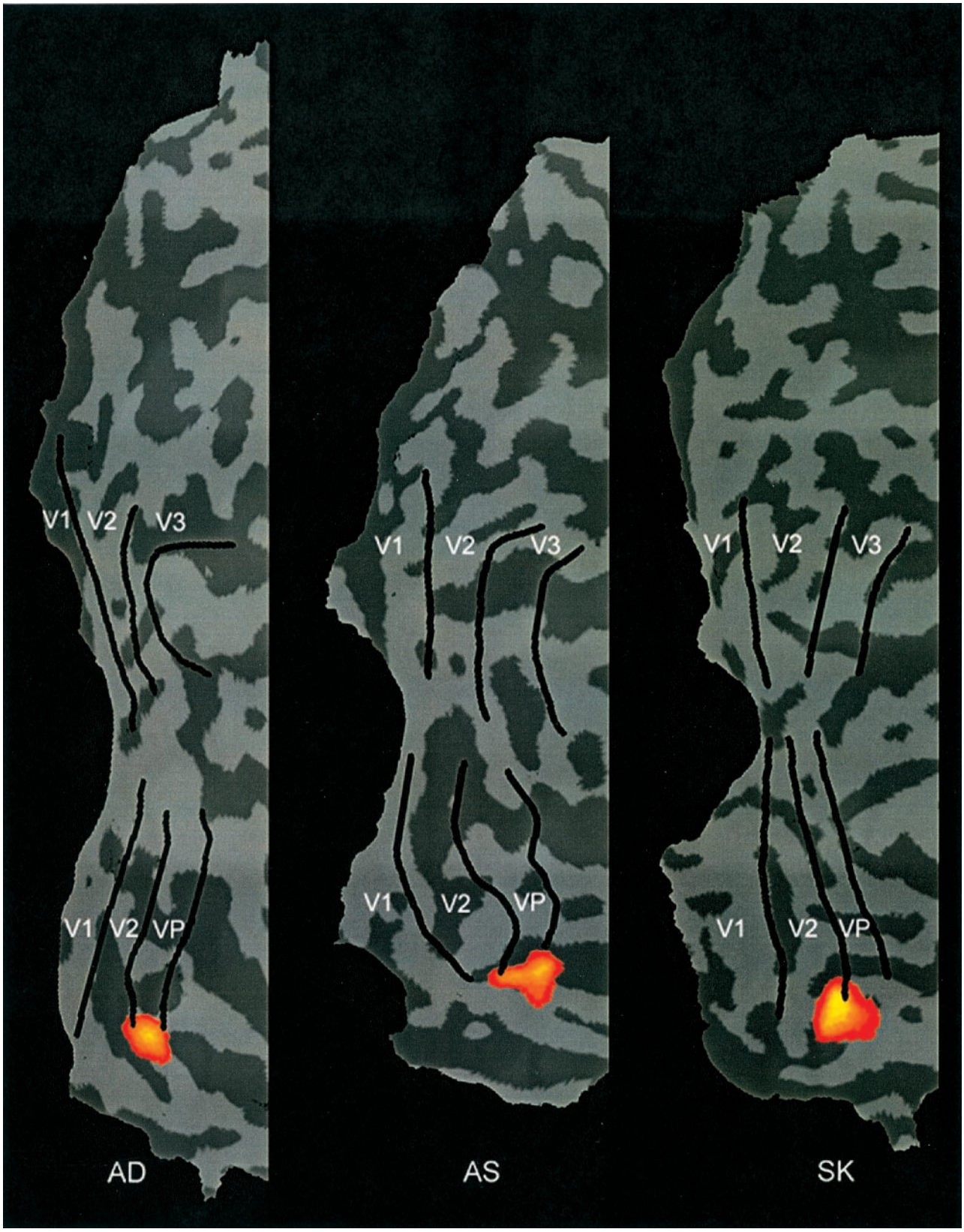

Figure 6. Activation for the biological motion with disturbance task for each subject (AD, AS and SK). The results are projected onto a flattened representation of the cortical surface of the right hemisphere. Overlaid on the cortical surface are also the borders of visual areas that have been identified with retinotopic methods.

lingual gyrus activation during the perception of biological motion. Moreover, the results suggest that this lingual gyrus activation is centered within area VP. The finding of activation within VP is consistent with the proposal by Zeki (Zeki, 1993) outlined in the Introduction. In addition, it refines his hypothesis by suggesting that it is the ventral portion of area V3 (area VP) that appears to play a special role in the perception of dynamic form such as biological motion.

General Discussion

Our main finding is that a region of the lingual gyrus, within area VP, is involved in biological motion processing. In experiment 1, we observed no overlap between the biological motion sensitive region and human area MT – the linear motion sensitive area – suggesting that our control stimuli were appropriate. The lack of overlap between the biological motion sensitive region and the frontal (precentral gyrus) and parietal (superior parietal lobule) regions involved in motor imagery suggests that the neural substrates of point-light body motion perception are different from those of motor imagery. Furthermore, the findings indicate that the neural substrates of point-light body motion perception are different from those of action perception (Decety and Grèzes, 1999) and those of apparent human movement perception (Stevens *et al.*, 2000).

Although most other biological motion neuroimaging studies do not report, or fail to emphasize, activation within the lingual gyrus, our finding is less surprising when one considers that several studies have demonstrated that the lingual gyrus appears to be involved in more specific aspects of motion processing than MT/MST. Orban *et al.* used PET to investigate the regions activated during speed discrimination tasks in comparison with simple motion detection tasks (Orban *et al.*, 1998). They showed that the right cuneus and right lingual gyrus, and to a lesser degree the left lingual gyrus and a more anterior lingual region in the right hemisphere, were involved in speed discrimination tasks, whereas the MT/MST complex did not show different activation between these tasks. Cornette *et al.* also showed a far greater involvement of lingual gyrus than the MT/MST complex in motion direction discrimination tasks than in simple detection tasks (Cornette *et al.*, 1998). These studies demonstrate that the same visual input and the same attribute (e.g. speed or direction of motion) produce different activation sites depending on whether or not a temporal comparison is required. Other studies have shown activation in the lingual gyrus during the observation of second-order motion compared with first-order motion (Smith *et al.*, 1998), and during the observation of motion-defined gratings, but not during the observation of static dots or unidirectional speed (Shulman *et al.*, 1998). These findings are consistent with the role of the lingual gyrus in such higher-level motion processing, as form-from-motion.

The neuroimaging study having the most similar methodology to ours is that conducted by Grossman *et al.* (Grossman *et al.*, 2000). Like our study, Grossman *et al.* used appropriate control stimuli (same local motion as biological motion stimuli) and an active task. Consistent with Grossman *et al.* (Grossman *et al.*, 2000), who reported STS activation in their group analyses, we observed 5 out of 10 subjects showing STG activation in one of our biological motion perception tasks. Unlike Grossman *et al.*, however, our group analysis did not result in a significant overall STG activation during the perception of point-light biological motion. Our group analysis did identify lingual gyrus activation in both of our biological motion perception tasks. Indeed, in experiment 1, 9 of our 10 subjects showed lingual gyrus activation during biological motion perception. The lack of lingual gyrus activation in Grossman *et al.*'s (Grossman *et al.*, 2000) study is somewhat puzzling since our study is quite similar. It is possible that any lingual gyrus activation that might have been present in their study would have been obscured by the relatively large (FWHM of 7.5 mm) spatial filter that they used to smooth their data.

The present findings in combination with previous work suggest that more than one cortical region is involved in the perception of biological motion – paralleling results in the face perception literature. As mentioned in the Introduction, in the monkey, neurons that respond selectively to faces are located in both the inferior temporal gyrus and on the bank of the STS. Human imaging studies also suggest involvement of two distinct areas (STS and fusiform gyrus) in face perception, which likely play different functional roles (Kanwisher *et al.*, 1997; Puce *et al.*, 1998). It is possible that the double dissociation found for face perception also holds true for biological motion perception. For example, the STS may be involved in providing the social meaning of biological motion stimuli [cf. (Allison *et al.*, 2000)] whereas the lingual gyrus (specifically area VP) may be involved in deriving biological forms from the motion information. It is noteworthy that the observation of meaningful hand actions has been shown to activate the STS while meaningless hand actions do not (Neville *et al.*, 1998).

We did not find activation in motor related, or motor imagery related, areas during observation of biological motion. This might be due to the nature of the biological motion perception tasks our subjects performed. Grèzes *et al.* (Grèzes *et al.*, 1998) showed that even when a subject is observing the same stimulus, areas of activation will differ depending on whether subjects are simply perceiving the stimuli or if they know that they will be asked to imitate the action later. Grèzes *et al.* (Grèzes *et al.*, 1998) found that when subjects perceived action with the aim to reproduce it later, the dorsal pathway and premotor cortex were more strongly activated than when they only perceived the same actions. It is understandable that we did not find activation in motor-related areas during the biological motion perception tasks because we did not require subjects to subsequently perform these movements.

Another area involved in the observation of action is the inferior frontal gyrus (Brodmann's areas 44/45). This appears to be the human homologue of monkey area F5 where mirror neurons (neurons that respond both when a particular action is performed by a monkey and when the monkey observes the same action performed by another individual) are found (Gallese and Goldman, 1998). Grèzes *et al.* (Grèzes *et al.*, 1998) found activation in these areas during observation of action with no purpose. We were unable to confirm this observation because the signal around these areas was distorted due to the air in the ear adjacent to these regions.

To summarize, the goal of the present study was to localize the brain regions involved in biological motion perception. In order to be confident that we were indeed localizing the critical brain regions, we developed biological motion displays and related control stimuli that had highly comparable local motion properties. We were able to identify a region in the lingual gyrus at the cuneus border that appears to be involved in the perception of biological motion. Furthermore, we replicated this finding in a second experiment that additionally determined the area to be within area VP. Given the findings from our study, and evidence from the functional neuroimaging, neuropsychological and single-cell recording literature, there is reason to believe that two regions are involved in biological motion perception: one

region centered around the STS and the other region centered within the lingual gyrus. These two regions are dissociable from cortical regions involved in the perception of linear motion, objects, and in the generation of motor imagery. These two spatially distinct regions may play complementary roles in the perception of biological motion. One area (lingual gyrus) may be involved in processing motion and deriving global form information while the other region (STG) may derive social meaning from this form-from-motion information. Future work will hopefully disambiguate the role of these two regions in biological motion perception.

Notes

We thank Dr Mel Goodale of the University of Western Ontario for continuing encouragement; Drs M. Riley, E. Nakano of ATR-I ISD and T. Yoshioka of ERATO for acquisition of biological motion data; and Joe Gati of the Robarts Research Institute for fMRI technical assistance. P.S. is supported by an NSERC operating grant and the Canada Research Chairs program.

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