UC San Diego

UC San Diego Previously Published Works

Title

Point-light biological motion perception activates human premotor cortex.

Permalink

https://escholarship.org/uc/item/47m2x3c8

Journal

The Journal of neuroscience, 24(27)

ISSN

1529-2401

Authors

Saygin, Ayse Pinar
Wilson, Stephen M
Hagler, Donald J
et al.

Publication Date

2004-07-07

Peer reviewed

eScholarship.org Powered by the California Digital Library
University of California

Point-Light Biological Motion Perception Activates Human Premotor Cortex

The Journal of Neuroscience, July 7, 2004 • 24(27):6181– 6188

Ayse Pinar Saygin,[1] Stephen M. Wilson,[2] Donald J. Hagler Jr.,[1] Elizabeth Bates,[1] and Martin I. Sereno[1]

[1] Department of Cognitive Science, University of California, San Diego, 9500 Gilman Drive, La Jolla, California, 92093-0515, USA.

[2] Ahmanson-Lovelace Brain Mapping Center and Neuroscience Interdepartmental Program, University of California, Los Angeles, California, 90095, USA.

Correspondence should be addressed to A.P. Saygin, asaygin@cogsci.ucsd.edu.

Abstract

Motion cues can be surprisingly powerful in defining objects and events. Specifically, a dozen or so point-lights attached to the joints of a human actor will evoke a vivid percept of action when the body is in motion. The perception of point-light biological motion activates posterior cortical areas of the brain. On the other hand, observation of others' actions is known to also evoke activity in motor and premotor areas in frontal cortex. In the present study we investigated whether point-light biological motion animations would lead to activity in frontal cortex as well. We carried out a human functional magnetic resonance imaging (fMRI) study on a high-field strength magnet and used a number of methods to increase signal, as well as cortical surface-based analysis methods. Areas which responded selectively to point-light biological motion were found in lateral and inferior temporal cortex and in inferior frontal cortex. The robust responses we observed in frontal areas indicate that these stimuli can also recruit action observation networks, even though they are very simplified and characterize actions by motion cues alone. The finding that even point-light animations evoke activity in frontal regions suggests that the motor system of the observer may be recruited to "fill in" these simplified displays.

Introduction

The perception of other individuals' movements and actions is important for tracking and hunting prey, detecting and avoiding predators, and in many species, social interaction. In humans and at least some other primates, premotor areas are involved in the perception of others' actions: recent research has shown that there are "mirror neurons" in the macaque frontal cortex in area F5 which fire during both action production and action perception (Gallese et al., 1996; Rizzolatti et al, 1996a; Rizzolatti et al., 2001; Ferrari et al., 2003). Studies on humans have also demonstrated the involvement of motor and premotor areas in action observation, indicating that humans may use information from their own body representations in understanding the actions of others (e.g., Fadiga et al., 1995; Grafton et al., 1996; Rizzolatti et al., 1996b; Decety et al., 1997; Iacoboni et al., 1999; Buccino et al., 2001; Grèzes et al., 2003).

Besides the visual perception of actions, other components of actions also drive neurons in premotor areas. Auditory mirror neurons respond to the sound of actions (such as the sound of a peanut cracking; Kohler et al., 2002), and "canonical neurons" respond to the target objects of actions (such as a visually presented peanut; Murata et al., 1997). The present study investigates whether premotor areas can be driven solely by motion cues of actions. It is possible to define actions by motion cues alone using "point-light biological motion". Image sequences constructed from a dozen point-lights attached to the limbs of a human actor can readily be identified as depicting actions, even though they do not define a form when stationary (Johansson, 1973). These animations convey surprisingly detailed information about movements of the human body, despite using motion signals almost exclusively, and lacking other visual cues such as color, shading and contours. Given that point-light biological motion figures depict actions, could their perception also recruit frontal cortex? Or are these stimuli too simplified to drive the neural activity in frontal action observation areas?

Previous neurophysiological and neuroimaging studies of point-light biological motion perception have not typically reported activations in frontal regions. Instead, areas identified in these studies include the superior temporal gyrus (STG) and sulcus (STS) (Grossman et al., 2000; Grèzes et al., 2001; Vaina et al., 2001; Beauchamp et al., 2003; Puce and Perrett, 2003), motion sensitive region MT and surrounding areas (MT+) (Grèzes et al., 2001; Vaina et al., 2001) parietal cortex (Bonda et al., 1996; Grèzes et al., 2001; Vaina et al., 2001), and other regions in visual cortex (Vaina et al., 2001; Servos et al., 2002).

In the present study, using fMRI, we investigated whether frontal action observation areas are involved in the perception of whole-body biological motion. Our approach was to use a relatively standard paradigm to identify regions in the brain which are responsive to biological motion. However, we used a combination of methods in our experimental design, fMRI acquisition, image processing, and data analysis to maximize signal in frontal cortex.

Materials and Methods

Participants

12 participants with no known visual or neurological abnormalities (7 females, aged 22-34) participated in the study. 11 participants were unaware of the main hypothesis of the study; one participant was an author. Subjects gave informed consent according to procedures approved by the Institutional Review Board of the University of California.

Experimental design and procedure

Participants were scanned as they viewed point-light biological motion animations, scrambled versions of the same animations, and stationary point-light figures. Scrambled animations, which contain the same local motion cues but not the form defined by biological motion, have been used as control stimuli in some prior studies of biological motion processing (e.g., Grossman et al., 2000; Servos et al., 2002). Because scrambled animations do not constitute actions, we would predict that an area that responds to the action information would respond significantly more to biological motion compared with the scrambled motion. We used a stationary point-light baseline condition so that activity during biological and scrambled motion could both be measured.

A blocked design was chosen to maximize statistical detection power (Liu et al., 2001), where the blocks consisted of biological motion, scrambled biological motion, and baseline (stationary point-light images). Figure 1 depicts several individual frames from each of these kinds of stimuli. During the scan, the three block types were presented in pseudo-randomized order and lasted 24 seconds each. There were 3 runs with 21 blocks in each run.

Point-light biological motion sequences were a subset of those used in Ahlstrom et al. (1997), and were created by videotaping an actor performing various activities and then encoding the joint positions in the digitized videos. 10 point-light actions were used in the present study, depicting walking, walking up stairs, jogging, jumping jacks, throwing, underarm throwing, skipping, stepping up, a high kick into the air, and a lower kick. Six identical point-light figures were displayed at all times, in order to maximize coverage of the visual field. The total area covered by the stimuli was approximately 16-18 degrees of visual angle in diameter (see Fig 1d). The animations were presented at 20 frames per second. Each animation was presented for 1 second with a delay of 250 msec between animations and an extra 250 msec interval between blocks. The joints of each point-light actor were represented by 12 small dots each subtending approximately 17 arc min of visual angle against a uniform dark background. For all point-light animations the visual spatial locations stimulated were maintained approximately the same. To achieve this, for the biological motion animations, when the action depicted motion which would normally result in the figure moving in space (e.g., walking), the point-light figure was adjusted such that the figure did not leave the region in which the animations were presented (e.g., the figure walked in place, as if on a treadmill). There was a small dark red crosshair at the center of the visual field to help subjects maintain central fixation and to minimize eye movements.

Scrambled animations were created by randomizing the starting positions of the point-lights while keeping the trajectories intact, except that each point-light could be randomly rotated in 90 degree increments and/or mirror-

inverted. The rotation and mirror inversion of dots during scrambling further disrupts local form information which may remain after spatial scrambling. The starting positions were chosen randomly within a region such that the total area encompassed by the figure was similar to that of the real figures. 10 scrambled animations and 10 static frames were used.

The experiment was programmed and run using MATLAB (Mathworks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were projected using an XGA video projector through a custom lens (Buhl Optical, Rochester, NY) onto a screen that was suspended above the subject's torso and was viewed through a mirror placed inside the head coil. We used an adjustable bite-bar to minimize head movements during the scan.

To control for differences in attention across conditions as much as possible, subjects were asked to carry out a simple task of judging whether the color of the point-lights in each trial were green or not; the task was the same regardless of stimulus type. Responses were collected with a Lumitouch button box (Photon Control, Burnaby, Canada).

Pilot data were acquired from individual subjects using alternate tasks or with no task before the present design was finalized; activation patterns observed in these pilot scans resembled those found in the results of the analyses reported here (see below). However, during passive observation scans, pilot subjects often reported feeling inattentive, so we used the color-monitoring task to keep subjects alert. The point-lights were presented only in white, green, or yellow, and the task was "green or not". The green and yellow colors were similar enough that sustained attention was required to avoid false alarms. This task was chosen because performance does not depend on the form of different visual stimuli so the subject's attention is focused on a feature of the stimulus (color) that can be varied in the same fashion across the three conditions (biological, scrambled, static). And finally, the task does not vary in difficulty across the different types of stimuli (confirmed in behavioral data, with accuracy in the task for biological motion: 98.2%, scrambled motion: 98.4%, static point-lights: 97.8%; $p > 0.05$ for all comparisons).

Many visual fMRI studies use 1-back working memory tasks to engage subjects' attention, which means that subjects monitor for repetitions of the visual stimuli as they are presented (e.g. Kanwisher et al., 1997). However, our pilot investigations and post-study subject interviews revealed that this task may not be ideal here since the difficulty of the working memory task varies by condition. To measure this more precisely, we asked 12 subjects to perform a 1-back working memory task with our three stimulus types outside the scanner. The results confirmed that indeed the 1-back task varies in difficulty for these stimuli. Accuracy was found to vary significantly by condition as follows: biological motion: 91.9%, scrambled motion: 87.0%, static point lights: 96.1% ($p < 0.05$ for all comparisons). In comparison to biological motion, the task is harder with scrambled motion, due to the unfamiliarity of the stimuli, and easier with static point-lights, since the final and initial frames of successive matching stimuli are identical. Since working memory tasks often activate frontal areas (Smith and

Jonides, 1999), such variation in task difficulty across conditions would complicate the interpretation of activity in frontal action observation areas.

Image acquisition

Scanning was carried out on a 4 Tesla Varian scanner equipped with a TEM transmit/receive head coil (Nova Medical, Wakefield, MA) at the UCSD Center for fMRI in La Jolla, CA. We acquired 3 runs of functional data (509 sec each) using a whole head EPI sequence (TR=2400 msec, TE=26.3, flip angle=90 degrees, 32 axial slices with interleaved acquisition, in-plane resolution of 3.75 mm and through-plane resolution of 3.8 mm with 0 mm gap). Experimental stimuli began after 3 TRs to allow the magnetization to reach steady state.

Given that this study was performed on a high field strength magnet, susceptibility effects were a significant concern and to help minimize these, we utilized a careful manual shimming routine, and adjusted both linear (n=3) and higher order (n=5) shims. In addition, a B0 field map (a set of multi-echo EPI images) was collected at the beginning of each scan session, after shimming, and was used to estimate the residual non-flatness of the B0 field. This data was then used to correct for magnetic field inhomogeneities which cause displacements in the phase-encode direction (Reber et al., 1998).

After functional scanning, a single structural volume for each subject was acquired using a T1-weighted magnetization-prepared rapid gradient echo (MPRAGE) sequence (TR=10.5 ms, TE=4.8, flip angle=11 degrees, 1×1×1.5 mm voxels). This structural scan was used as an intermediate step in spatially aligning the functional images to high resolution (1×1×1 mm) T1-weighted MPRAGE scans previously obtained on a 3-Tesla Varian scanner or a 1.5-Tesla Siemens Vision clinical scanner. These earlier-obtained high-resolution scans were used to reconstruct the cortical surface of each subject as described previously (Dale et al., 1999; Fischl et al., 1999a).

Image Processing and Analysis

Image preprocessing and statistical analysis were performed using Analysis of Functional Neuroimages (AFNI) (Cox, 1996) and FreeSurfer (Dale et al., 1999; Fischl et al., 1999a) software packages.

For each individual subject, the B0 field maps were used to correct for distortions in the phase-encode direction using in-house software developed at the UCSD fMRI center by L. Frank. The 3 runs were concatenated (yielding 630 volumes) and spatially registered in three-dimensional space for motion correction using AFNI programs. Estimates of the three translation and three rotation parameters were computed during this registration and saved. The AFNI program 3dDeconvolve was used to fit a general linear model at each voxel. The model contained four parameters for each of the two non-baseline conditions, modeling hemodynamic responses at different lag times (0 to 3 TRs), three parameters for each run to account for slow drifts, and the six motion vectors as determined during motion correction. For individual subject analyses, the contrast between the two conditions (biological vs. scrambled motion) was performed by using F-tests to compare the sums of the four parameters (i.e., the areas under the fitted hemodynamic response functions).

The group data was analyzed using cortical surface-based methods (Dale et al., 1999; Fischl et al., 1999a, 1999b). Each subject's cortical surface was reconstructed, then morphed to an average spherical representation of

the cerebral hemispheres that optimally aligns the sulcal and gyral features across subjects through a procedure which aims to match anatomically homologous areas across subjects while minimizing metric distortion (Fischl et al., 1999b). To perform functional analysis on the sphere, first each subject's volume-based individual statistical maps of coefficients were interpolated onto the spherical representation of their hemispheres using FreeSurfer. Then these maps were morphed and resampled onto the common spherical space. At this stage, 50 steps of spatial smoothing on the spherical surface were applied; we carried out simulations with a set of surfaces and a set of points on the cortex, and found this to correspond approximately to a Gaussian filter with FWHM of 7 mm alongside the cortical surface (A.P. Saygin and D.J. Hagler, unpublished simulations). A 2-factor analysis of variance (ANOVA) was carried out on the spherical surface using a mixed effects model with condition as the fixed effect and subjects as the random effect. The resulting statistics were then transferred onto the inflated cortical surface of a single subject for display.

In order to examine responses to biological motion and scrambled biological motion more closely, we also defined regions of interest (ROI) and examined the responses in these areas. We selected inferior frontal (IF) and premotor (Prem) cortical regions as our main regions of interest based on these areas' previously known involvement in action observation. We also studied the posterior superior temporal sulcal (pSTS) region, as it is an area known to respond to point-light biological motion. These ROIs were drawn on the cortical surface of each hemisphere of each individual subject using FreeSurfer and saved as surface patches. Anatomical criteria were as follows: The IF ROI contained the inferior frontal gyrus (IFG) and the inferior frontal sulcus (IFS) and was bounded by (but did not contain any cortex from) the middle frontal gyrus, precentral sulcus, lateral orbital sulcus, and the Sylvian fissure. The Prem ROI was drawn on the lateral cortical surface and consisted of the precentral gyrus and the posterior bank of the precentral sulcus, but did not extend into the middle and superior frontal gyri, or the central or inferior frontal sulci. While most action observation studies have observed responses in ventral portions of premotor cortex, it is also known that responses in premotor cortex during observation of body actions may be somatotopically specific (Buccino et al., 2001). Since our stimuli contain actions of the whole body, we found it appropriate to include the whole lateral extent of the precentral region in order to cover a large extent of human premotor cortex rather than only the more ventral portions corresponding mostly to the arm and hand representations. This ROI did not extend into the medial surface of the precentral gyrus. Finally, the pSTS ROI was drawn to include the posterior half of the superior temporal sulcal cortex.

For these three anatomical ROIs, time courses were extracted based on voxels which were responsive to motion – either biological or scrambled – at $p < 10^{-3}$. Since the design of the experiment was a mixed block design (in order to maximize signal), biological motion and scrambled motion blocks could follow each other and thus the hemodynamic responses to each kind of stimulus could overlap. Thus, in order to extract the BOLD responses corresponding to each condition in our experiment, we used the AFNI program 3dDeconvolve: The mean time course from each ROI of each hemisphere was averaged and deconvolved with a model containing 16 parameters each for the biological motion and the scrambled motion conditions corresponding to stimulus time points

throughout the experiment (10 TRs per block, the 2 TRs preceding each block and the 4 TRs following each block). The extracted BOLD responses for biological motion and scrambled biological motion across the 16 time points were then averaged across subjects for each ROI and hemisphere, resulting in average estimated BOLD responses for biological motion and scrambled biological motion blocks.

Results

The group results for the 12 subjects are depicted in Figure 2. We first discuss responses to biological motion and scrambled biological motion compared with the static baseline (Fig. 2a and 2b), before moving to the main comparison of interest, which is the contrast between biological motion and scrambled motion (Fig. 2c). The activations against baseline are important because they illustrate the areas that respond to both biological and scrambled motion, which cannot be inferred from a difference image.

When biological motion observation was compared to the static point-light observation baseline (Fig. 2a), we found a robustly responsive region along the inferior frontal and precentral sulci bilaterally, indicating that point-light animations indeed recruit frontal areas known to be involved in action observation. This activation followed inferior frontal and precentral sulci in a fairly continuous manner but Talairach coordinates of the most significantly responsive points in the inferior frontal, inferior precentral and superior precentral sulci are reported online in Supplementary Table 1.

In posterior brain regions, compared to the static baseline condition, biological motion led to extensive activation in occipital, temporal, and parietal cortex, extending along both the ventral and dorsal visual streams. Since many of these regions were also responsive to scrambled motion (see below), motion processing may account for much of this activity. The peak of this continuous extensive response was in the lateral temporal cortex, inferior to the STS, near anatomical areas which are known to respond strongly to motion stimuli (human MT, MST and surrounding regions, henceforth MT+). Peak coordinates here, and in the pSTS, intraparietal sulcus (IPS), inferotemporal cortex, and the posterior insular cortex (which has been considered the putative human analog of the monkey parietoinsular vestibular cortex or PIVC, see Güldin & Grusser, 1998 for review) are reported in Supplementary Table 1.

Scrambled biological motion, relative to the static point-light baseline, activated many of the same regions as biological motion in occipital, temporal, parietal and posterior insular cortex, although the activation was noticeably less extensive (Fig. 2b, see also Supplementary Table 1 for coordinates of activation peaks). The most significant responses were once again in posterior lateral temporal cortex around MT+, reflecting motion processing. On the other hand, scrambled biological motion did not evoke much activation in frontal cortex even in comparison with baseline, and even at low thresholds. Indeed, no difference was visible between scrambled motion and the static baseline in the left hemisphere. In the right hemisphere a small area of activation in the precentral sulcus associated with scrambled motion against baseline was found, but this was weaker and less extensive than the activation seen for biological motion.

When biological motion and scrambled biological motion responses were compared directly, we found that a region in the left inferior frontal sulcus (IFS), at its junction with and partially extending into the precentral sulcus, responded significantly more to biological motion (Fig. 3c). In fact, this was the most significantly responsive area for this contrast in the whole brain (peak Talairach coordinates (-41, 14, 18) with t=9.8). There were less significant peaks in the inferior precentral sulci bilaterally (left hemisphere peak at (-37, 5, 25) with t=5.5 and right hemisphere peak at (34, 7, 27) with t=5.2). Thus, we found support for the hypothesis that motion information in body actions can drive neural activity in frontal cortical regions.

In line with prior work, we also found lateral temporal regions that responded more strongly to biological motion than to scrambled motion. Although the peak voxels were in rather similar locations in the two hemispheres, (see Supplementary Table 1), the region that was significantly responsive to the contrast extended more anteriorly and superiorly towards the STS in the left hemisphere and while these areas were responsive in the right hemisphere as well, the strongest responses lay more posteriorly in this hemisphere. Finally, a region in left ventrolateral inferotemporal cortex (most anterior activation in temporal cortex seen in Fig. 2c) also showed significant responses to biological motion compared with scrambled biological motion. We did not find brain areas which preferred scrambled motion over biological motion.

Note that the large activated regions in temporal cortex likely contain multiple functional visual areas as they are very close to or partially overlapping with areas which have been reported in previous studies to be responsive to simple motion (e.g., Tootell et al., 1995), visual form of objects (e.g., Grill-Spector et al., 1999), human bodies (e.g., Downing et al., 2001), as well as to shape-from-motion (e.g., Murray et al., 2003). In fact, we verified this by examination of several individual subjects' biological motion responsive regions identified in this study in relation to results from localizer scans carried out in our laboratory, and found that at the individual subject level, brain areas which have a preference for biological motion have considerable overlap with areas which respond to simple motion, object form, human faces, and especially, human body form (data not shown). Additionally, while a large area in lateral temporal is cortex responsive to biological motion, it has also been observed that different portions of human temporal cortex have relative preferences for different kinds of motion stimuli, for example biological versus artifact motions (see, Beauchamp et al., 2003; Pelphrey et al., 2003).

We next examined the average hemodynamic responses to the biological motion and scrambled biological motion blocks across the 12 subjects for two anatomical regions in frontal cortex which are known to respond during action observation: inferior frontal cortex (IF) and premotor (Prem) cortex. We also studied the posterior superior temporal sulcal region (pSTS) as it is known to respond more to biological motion than scrambled biological motion (see Methods for anatomical boundaries of these ROIs). Figure 3 depicts the percent signal change for each of these ROIs in each of the two hemispheres.

In contrast to most previous studies, the addition of a baseline condition in our experiment (stationary point-light observation while executing the color-monitoring task) allowed us to examine responses to both biological and scrambled motion. In all ROIs in both hemispheres, responses to biological motion were much larger

than the responses to scrambled motion, although scrambled motion can also be seen to give rise to responses significantly above baseline in all regions. The amplitude of the signal change in pSTS was greatest, which is not unexpected since this is a posterior brain area known to be involved in the visual perception of biological motion. Signal change in pSTS for scrambled motion was also quite high but the area showed a stronger response to the biological motion stimuli, as has been observed previously (e.g., Grossman et al., 2000). Responses in frontal cortex were also strong. We found very similar response patterns to those in pSTS in both the IF and the Prem ROIs: the percent signal change in these regions for biological motion was much greater than that for scrambled biological motion. Moreover the difference in the responses to the two stimulus types in frontal cortex was similar in magnitude to the difference observed in the pSTS. To quantify this, we calculated the area under the estimated hemodynamic response curves for the biological and scrambled motion conditions, and we found that the size of the response in the scrambled motion condition as a fraction of the response in the biological motion condition was very similar across ROIs: IF: 56.3%; Prem: 55.7%; pSTS: 58.6%. This suggests that the frontal regions are just as selective for biological motion as the pSTS.

As with most fMRI studies, group analyses show the strongest and most reliable responses to biological motion across a group of subjects, whereas for individual subjects there is some variability in the activation patterns obtained. In Figure 4 we show biological versus scrambled motion contrasts for three individual subjects with varying amounts and differing patterns of activations. There were some subjects who showed significant responses to biological motion compared with scrambled biological motion in parietal cortex (e.g., Subjects 2 and 3), consistent with some previous results (Bonda et al., 1996 (only for hand actions); Grèzes et al, 2001; Vaina et al., 2001). In some individual subjects, the response extended ventrally towards inferotemporal cortex (e.g., Subject 3 and in the left hemisphere of Subject 2; the extension is partially visible in the lateral view, ventral view not shown) which has also been reported in some prior studies (Vaina et al., 2001; Grossman and Blake, 2002). The frontal response, which is the focus of this study, also showed some variability. Most notably, several subjects' frontal activation extended dorsally along the precentral sulcus, beyond the IFS focus which emerged from the group average as the most responsive region to biological motion (Subjects 1, 2 and 3). Other subjects had activation in slightly more anterior or inferior regions of the IFS (Subject 2, and a smaller focus seen in the left hemisphere of Subject 1). For some subjects the response in the posterior insula (or human PIVC) showed a significant difference between biological and scrambled motion (e.g., seen bilaterally in Subjects 2 and 3).

Finally, overlaid on the activation maps for subject 3 are the areas activated in a separate scanning session for biological versus scrambled motion as this subject performed a 1-back working memory task instead of the color monitoring task. As noted above, behavioral data indicate that the 1-back task is more difficult for scrambled motion, presumably because the items to be compared are unfamiliar. However, the areas activated were very similar across the two tasks; in particular, the IFS and premotor cortex responded significantly more strongly to biological motion during the 1-back task. Also shown is average percent signal change in each of the three ROIs (IF, Prem and pSTS, right and left hemispheres averaged) for each task. In each ROI, the response pattern

(biological motion > scrambled motion) was the same regardless of the task. These results suggest that the activated frontal areas are unlikely to reflect general attentional differences between the conditions, since the 1-back task is more challenging for the scrambled condition and hence presumably places greater demands on working memory, executive and attentional systems, yet even in this case the IFS and premotor regions respond more strongly to biological motion.

Discussion

This study aimed to investigate whether frontal areas known to be activated by action observation would respond also to actions characterized solely by motion cues. We used point-light biological motion animations of whole body actions which have consistently activated superior temporal cortical areas in most prior human neuroimaging studies (Beauchamp et al., 2003; Bonda et al, 1996; Grossman et al., 2000; Grèzes et al, 2001; Vaina et al., 2001; although see Servos et al., 2002). Our approach was to keep the experimental design straightforward (block design with two motion conditions and one static baseline, using a simple task), but to use a combination of methods to increase the signal from frontal cortex.

We found that frontal cortex showed a robust response to point-light biological motion. In comparison to static point-lights, there was activation that followed the precentral and inferior frontal sulci bilaterally. Frontal areas also showed selective responsivity to biological motion compared to scrambled biological motion. These results support the view that perception of the motion information in body actions can drive inferior frontal and premotor areas involved in action perception.

When we investigated the MR signal in IF, Prem and pSTS ROIs, we saw that the BOLD response in frontal areas showed a very similar pattern to that in pSTS, an area whose importance in biological motion processing is already established. More precisely, IF and Prem were as selective as pSTS to the contrast between biological and scrambled motion as revealed by both the surface based group analysis and the ROI analyses.

Frontal cortical areas (as well as sensory areas in other parts of the brain) are known to be modulated by attention (see Pessoa, Kastner & Ungerleider, 2003 for review). However the frontal areas observed in our study are unlikely to mainly reflect differences in attention across the conditions. A 1-back working memory task, which is more attentionally demanding for the scrambled condition, revealed the same pattern of responses (biological>scrambled) in the inferior frontal and precentral areas activated with the “neutral” color monitoring task. Another consideration is that the areas activated in this study overlap only partially with areas thought to be important for attentional control. The very dorsal extent of the premotor activity we observed likely overlaps with the location of the frontal eye fields near the junction of the superior frontal sulcus and superior precentral sulcus (Paus, 1996), and attention shifts have also been reported to activate an area in the inferior precentral sulcus (Beauchamp et al., 2001). But the IFS, where we saw the largest differences between biological and scrambled motion in the surface-based group analysis, is not thought to be involved in spatial attentional processes.

The present study is the first study which shows a clear response to point-light biological motion animations in frontal areas known to be involved in action observation, although there are a few related results from prior studies. First, we found inferior frontal lesion sites (as well as superior temporal and parietal sites) to be implicated in biological motion perception deficits in a group of unilateral stroke patients (A.P. Saygin and S.M. Wilson, unpublished observations). Second, right lateralized frontal activation in Brodmann area (BA) 47 and extending into BA 45 was found in a previous fMRI study of biological motion processing (Vaina et al., 2001). However, in that study subjects were viewing both biological and scrambled biological motion stimuli within a single condition and performing a discrimination task between the two kinds of motion, which makes the interpretation of this activation difficult. Santi et al. (2003) also reported activation in BA 47 in the right hemisphere during biological motion perception. Note that BA 47 is inferior and anterior to regions typically active during action observation. In the same study, a large region of frontal activation overlapping with known action observation networks in the left hemisphere was found to be responsive to point-light biological motion. However, this area was responsive only to visible speech biological motion as subjects were trying to lip-read, and did not respond during observation of whole-body biological motion actions. Based on these results, the authors suggested that the activation in these premotor and motor regions was linguistically specific. The present study however shows that body actions also evoke activity in these frontal regions. We suggest instead the linguistic task they used (lip-reading) may have led to the relative differences they observed between speech and non-speech biological motion observation.

In sum, while frontal cortical involvement has sometimes been observed in prior studies involving biological motion, no previous imaging study has shown responses specific to point-light biological motion actions in frontal areas known to be involved in action observation. Methodological differences between previous neuroimaging studies that examined biological motion perception and our experiment may account for the different results we obtained. First, we used a color detection task as opposed to passive viewing or a working memory task. Second, we presented multiple point-light animations at any given time. Finally, and probably most importantly, we took additional steps to maximize signal in our fMRI design, acquisition and analysis methods (e.g., used a 4 Tesla scanner, B0 field map correction, linear and higher order shimming, and surface-based intersubject averaging methods).

Where do the frontal regions activated in our study lie in relation to areas identified in prior studies of action observation? Many action observation and imitation studies have pointed to the posterior inferior frontal gyrus (IFG) as being a particularly important area and a possible homologue for macaque area F5 which contains mirror neurons (Rizzolatti et al., 2001). Several action observation and imagery studies have found responses in premotor areas as well (see Jeannerod, 2001 for review). We plotted on the cortical surface several reported peak activation coordinates from previously published studies that had action observation conditions and that found responses in inferior frontal cortex (Grafton et al., 1996; Rizzolatti et al., 1996b; Decety et al., 1997; Iacoboni et al., 1999; Grèzes et al., 2003). Several of these foci fell on the IFG, a few millimeters to a centimeter inferior to our

activation (Grafton et al., 1996; Rizzolatti et al., 1996b; Iacoboni et al., 1999); one was a few millimeters anterior to our focus again on the IFG (Decety et al., 1997); and one study reported a focus which is overlapping with our biological motion responses (Grèzes et al., 2003). However, since the reported peaks are points in the center of an activated region, they may still overlap with our responses.

Does this localization in the present study to the IFS rather than to the IFG have any significance? We suggest three possible reasons for the differences in precise localization. Firstly, there are methodological differences between studies. The present study employed surface-based group registration, which aims to optimally align particular sulci and gyri. The localization to the sulcus in the group results follows from the fact that the activation was generally localized to the sulcus for each individual subject. Secondly, the difference might depend on the fact that the actions in the present study were defined by motion alone, whereas previous action observation studies have used videotaped actions which contain many other visual cues such as form, contour and color. It may be that slightly different frontal areas are engaged by different aspects of action perception. Thirdly, and perhaps most likely, most previous studies have used hand action stimuli (e.g., grasping) whereas in the present study whole body actions were used to maintain contiguity with the previous literature on point-light biological motion processing. It has been shown that action observation activates premotor areas in a somatotopic manner (Buccino et al., 2001); therefore it may be expected that actions involving different body parts would activate different regions. Since hand motor representations are ventral to representations for many body parts such as the arms, shoulders, trunk and legs (Preuss et al., 1996), the more superior focus that we observed could be due to the fact that our stimuli contained whole body movements.

Finally, is noteworthy that in the macaque, mirror neurons in premotor cortex respond only to real actions performed in front of the monkey and not even to videotaped actions (e.g., see Ferrari et al., 2003), whereas human premotor cortex responds even to point-light biological motion representing actions. This contrast between humans and macaques suggests that the human mirror neuron system may be more capable of processing abstract visual representations of actions.

While others' actions are most often experienced through the visual system, an organism's own experience of performing the same action will involve motor, sensory and proprioceptive representations (Barresi and Moore, 1996). A unified representation of action requires that perceived actions and performed actions be related to each other in the brain, even though they are often experienced through different sensory modalities. In this context, the discovery that perception of actions can engage neural systems involved in production of actions has been an exciting development. The present study showed that human premotor cortex responds during the perception of actions defined by motion cues alone. Our findings suggest that we may be filling in these simplified animations using information from our own motor system, lending support to an analysis-by-synthesis view of action perception.

Author Note: Elizabeth Bates, professor of Cognitive Science at the University of California, San Diego, passed away December 13, 2003.

Acknowledgments: This research was supported by NSF BCS 0224321 (Sereno) and NIH RO1 DC00216 (Bates). We thank R. Buxton, L. Frank, T. Liu, E. Wong from the UCSD Center for fMRI for their support and pulse sequence, hardware and software development, E. Grossman for sharing stimuli, and M. Iacoboni, F. Dick and the anonymous reviewers for their comments.

References

Ahlstrom V, Blake R, Ahlstrom U (1997) Perception of biological motion. Perception 26:1539–1548.

Barresi J, Moore C (1996) Intentional relations and social understanding. Behav Brain Sci 19:107–122.

Beauchamp MS, Lee KE, Haxby JV, Martin A (2003) FMRI responses to video and point-light displays of moving humans and manipulable objects. J Cogn Neurosci 15:991–1001.

Beauchamp MS, Petit L, Ellmore TM, Ingeholm J, Haxby JV (2001) A parametric fMRI study of overt and covert shifts of visuospatial attention. Neuroimage 14:310–321.

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

Brainard DH (1997) The Psychophysics Toolbox. Spat Vis 10:433–436.

Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur J Neurosci 13:400–404.

Cox RW (1996) AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. Comput Biomed Res 29:162–173.

Dale AM, Fischl B, Sereno MI (1999) Cortical surface-based analysis. I. Segmentation and surface reconstruction. Neuroimage 9:179–194.

Decety J, Grèzes J, Costes N, Perani D, Jeannerod M, Procyk E, Grassi F, Fazio F (1997). Brain activity during observation of actions: Influence of action content and subject's strategy. Brain 120:1763–1777.

Downing PE, Jiang Y, Shuman M, Kanwisher N (2001) A cortical area selective for visual processing of the human body. Science 293:2470–2473.

Fadiga L, Fogassi L, Pavesi G, Rizzolatti G (1995) Motor facilitation during action observation: a magnetic stimulation study. J Neurophysiol 73:2608–2611.

Ferrari PF, Gallese V, Rizzolatti G, Fogassi L (2003) Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. Eur J Neurosci 17:1703–1714.

Fischl B, Sereno MI, Dale AM (1999a) Cortical surface-based analysis. II: Inflation, flattening, and a surface-based coordinate system. Neuroimage 9:195–207.

Fischl B, Sereno MI, Tootell RB, Dale AM (1999b) High-resolution intersubject averaging and a coordinate system for the cortical surface. Hum Brain Mapp 8:272–284.

Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. Brain 119:593–609.

Grafton ST, Arbib MA, Fadiga L, Rizzolatti G (1996) Localization of grasp representations in humans by positron emission tomography: 2. Observation compared with imagination. Exp Brain Res 112:103–111.

Grèzes J, Fonlupt P, Bertenthal B, Delon-Martin C, Segebarth C, Decety J. Does perception of biological motion rely on specific brain regions? Neuroimage 13:775–785.

Grèzes J, Armony JL, Rowe J, Passingham RE (2003) Activations related to "mirror" and "canonical" neurones in the human brain: an fMRI study. Neuroimage 18:928–937.

Grill-Spector K, Kushnir T, Edelman S, Avidan G, Itzchak Y, Malach R (1999) Differential processing of objects under various viewing conditions in the human lateral occipital complex. Neuron 24:187–203.

Grossman ED, Blake R (2002) Brain areas active during visual perception of biological motion. Neuron 35:1167–1175.

Grossman E, Donnelly M, Price R, Pickens D, Morgan V, Neighbor G, Blake R (2000) Brain areas involved in perception of biological motion. J Cogn Neurosci 12:711–720.

Güldin WO, Grusser OJ (1998) Is there a vestibular cortex? Trends Neurosci. 21:254–259.

Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G (1999) Cortical mechanisms of human imitation. Science 286:2526–2528.

Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. Neuroimage 14:S103–S109.

Johansson G (1973) Visual perception of biological motion and a model for its analysis. Percept Psychophys 14:201–211.

Kanwisher N, McDermott J, Chun MM (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 17:4302–4311.

Kohler E, Keysers C, Umilta MA, Fogassi L, Gallese V, Rizzolatti G (2002) Hearing sounds, understanding actions: action representation in mirror neurons. Science 297:846–848.

Liu TT, Frank LR, Wong EC, Buxton RB (2001) Detection power, estimation efficiency, and predictability in event-related fMRI. Neuroimage 13: 759–773.

Murata A, Fadiga L, Fogassi L, Gallese V, Raos V, Rizzolatti G (1997) Object representation in the ventral premotor cortex (area F5) of the monkey. J Neurophysiol 78:2226–2230.

Murray SO, Olshausen BA, Woods DL (2003) Processing shape, motion and three-dimensional shape-from-motion in the human cortex. Cereb Cortex 13:508–516.

Paus T (1996) Location and function of the human frontal eye-field: A selective review. Neuropsychologia 34, 475–483.

Pelli DG (1997) The Video Toolbox software for visual psychophysics: transforming numbers into movies. Spat Vis 10:437–442.

Perani D, Fazio F, Borghese NA, Tettamanti M, Ferrari S, Decety J, Gilardi MC (2001) Different brain correlates for watching real and virtual hand actions. Neuroimage 14:749–758.

Pelphrey KA, Mitchell TV, McKeown MJ, Goldstein J, Allison T, McCarthy G (2003) Brain activity evoked by the perception of human walking: controlling for meaningful coherent motion. J Neurosci 23:6819–6825.

Pessoa L, Kastner S, Ungerleider LG (2003) Neuroimaging studies of attention: from modulation of sensory processing to top-down control. J Neurosci 23: 3990–3998.

Preuss TM, Stepniewska I, Kaas JH (1996) Movement representation in the dorsal and ventral premotor areas of owl monkeys: a microstimulation study. J Comp Neurol 371:649–676.

Puce A, Perrett D (2003) Electrophysiology and brain imaging of biological motion. Philos Trans R Soc Lond B Biol Sci 358:435–445.

Reber PJ, Wong EC, Buxton RB, Frank LR (1998) Correction of off resonance-related distortion in echo-planar imaging using EPI-based field maps. Magn Reson Med 39:328–330.

Rizzolatti G, Fadiga L, Gallese V, Fogassi L (1996a) Premotor cortex and the recognition of motor actions. Brain Res Cogn Brain Res 3:131–141.

Rizzolatti G, Fadiga L, Matelli M, Bettinardi V, Paulesu E, Perani D, Fazio F (1996b) Localization of grasp representations in humans by PET: 1. Observation versus execution. Exp Brain Res 111:246–252.

Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. Nat Rev Neurosci 2:661–670.

Santi A, Servos P, Vatikiotis-Bateson E, Kuratate T, Munhall K (2003) Perceiving biological motion: dissociating visible speech from walking. J Cogn Neurosci 15:800–809.

Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ, Rosen BR, Tootell RB (1995) Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. Science 268, 889–893.

Servos P, Osu R, Santi A, Kawato M (2002) The neural substrates of biological motion perception: an fMRI study. Cereb Cortex 12:772–782.

Smith EE, Jonides J (1999) Storage and executive processes in the frontal lobes. Science 283:1657–1661.

Thornton IM, Rensink RA, Shiffrar M (2002) Active versus passive processing of biological motion. Perception 31:837–853

Tootell RB, Reppas JB, Kwong KK, Malach R, Born RT, Brady TJ, Rosen BR, Belliveau JW (1995) Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. J Neurosci 15:3215–3230.

Vaina LM, Solomon J, Chowdhury S, Sinha P, Belliveau JW (2001) Proc Natl Acad Sci USA 98:11656–11661.

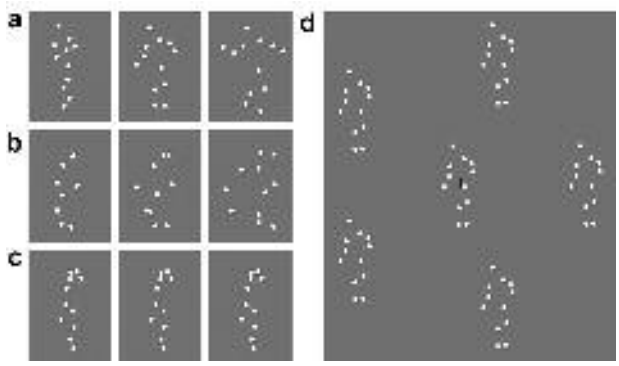

Figure 1. Example frames for the three stimulus conditions. Three (out of twenty) frames are shown from one animation each for **a**) biological motion, **b**) scrambled biological motion, **c**) static point-lights (baseline) conditions in the experiment. The biological motion animation in this example depicts frames from an actor throwing an object (e.g., a ball). The static point-lights condition does not have any motion and hence all frames are the same. In **d)** an example screenshot from the actual experiment (biological motion condition) is shown. All six copies of the figure executed the same motion.

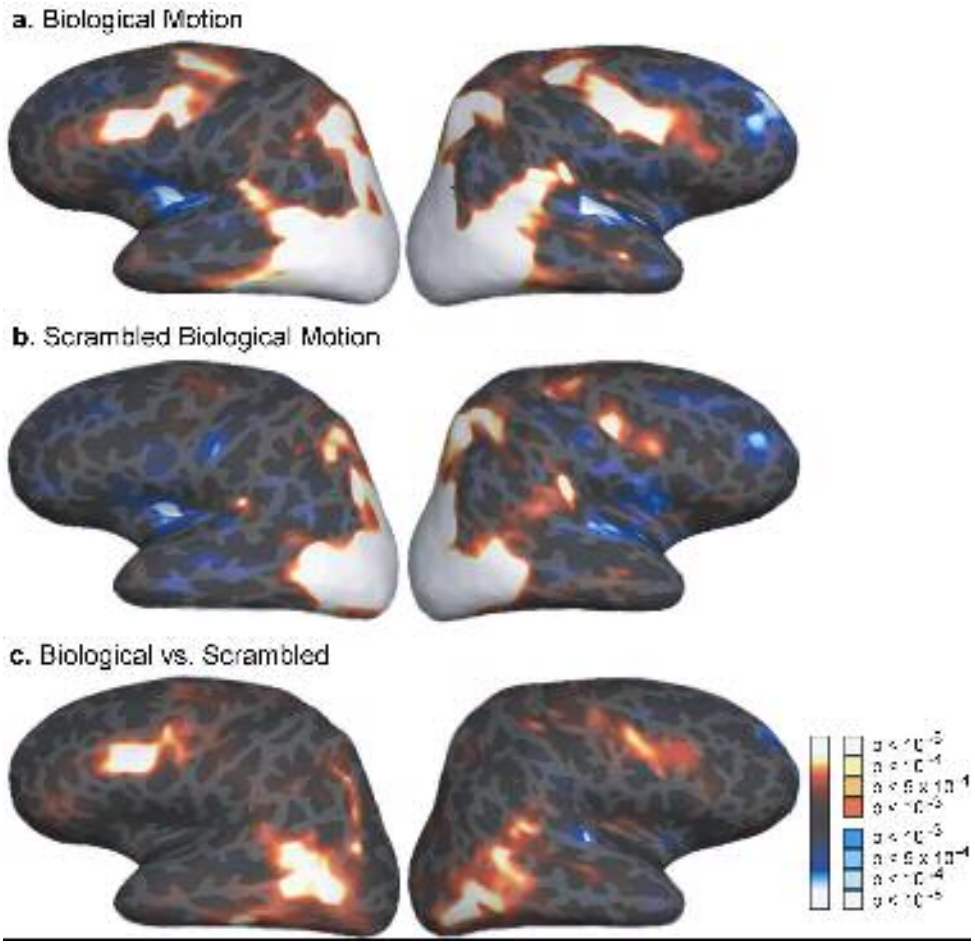

Figure 2. Results of group analyses. Surface-averaged group ANOVA results are displayed on the lateral views of the inflated cortical hemispheres of a single subject for **a**) biological motion (vs. baseline), **b**) scrambled biological motion (vs. baseline), and **c**) biological motion vs. scrambled biological motion contrast. The color bar displays the colors in the images and the discrete swatches mark colors which correspond to *p*-values smaller than 10^{-3}, $5x10^{-4}$, 10^{-4}, and 10^{-5}, or $|t|>4.4$, $|t|>4.8$, $|t|>5.9$, and $|t|>7.6$, respectively. Note that the same color scale is used to depict the results for the activations against baseline (**a** and **b**) and the activation differences between the two motion stimuli (**c**). See Supplementary Table 1 for coordinates of peak activations.

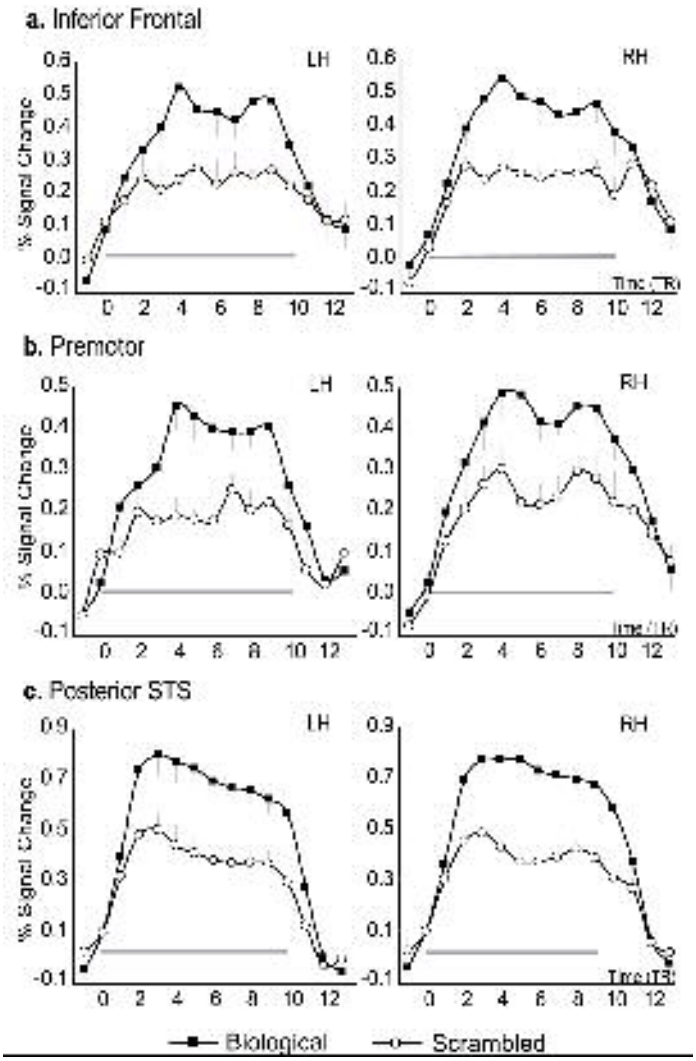

Figure 3. Percent MR signal change across time for the biological motion and scrambled biological motion blocks in the IF, Prem and pSTS regions of interest. The filled squares depict the signal for biological motion and the empty circles for scrambled motion. The error bars show standard error across the 12 subjects. In IF, mean number of voxels included in the ROI analyses across the 12 subjects was 53 in LH, 58 in RH; in Prem 64 in LH, 80 in RH; in pSTS 108 in LH, 98 in RH. The horizontal gray line marks actual duration of stimuli (10 TRs or 24 seconds).

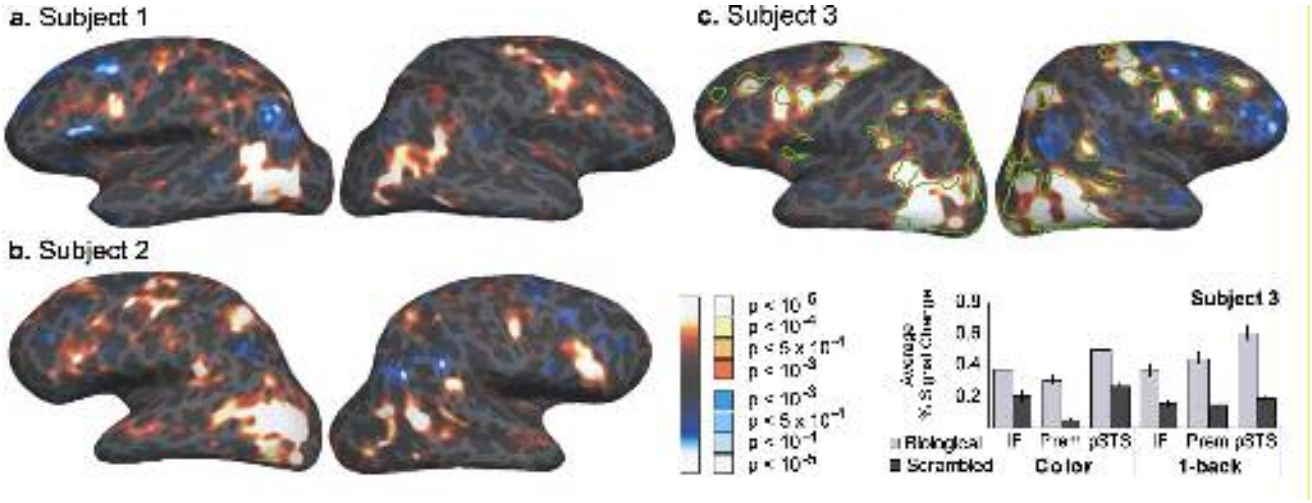

Figure 4. Example individual subject results. Results for the biological motion vs. scrambled biological motion contrast is shown on inflated lateral views of three subjects' hemispheres. The color bar shows the colors in the images and the discrete swatches mark colors which correspond to *p*-values smaller than 10^{-3}, $5x10^{-4}$, 10^{-4}, and 10^{-5}, or $|t|>3.3$, $|t|>3.5$, $|t|>3.9$, and $|t|>4.5$, respectively. In **a**) Subject 1 can be seen to show a pattern similar to the frontal and temporal response pattern found in the group study, with more extension into precentral sulcus. In **b)** and **c)** Subject 2 and Subject 3 are depicted showing strong activity in inferior frontal and premotor areas in frontal cortex in addition to superior temporal, parietal, posterior insular and inferotemporal cortex (left lateralized for Subject 2, bilateral for Subject 3 with extension into ventral cortex, which is not visible). In **c)** additional data for Subject 3 is shown from a separate scan in which the same stimuli were presented in a 1-back working memory task with different attentional requirements. In order to show precise alignment of activated regions in the two different tasks, regions responsive to the biological motion vs. scrambled biological motion contrast during the 1-back task at $p<10^{-3}$ are outlined in green and superimposed onto the surface on which the data from the main experiment (color-monitoring task) was rendered. Also shown in **c)** is a graph of the average percent signal change in our three ROIs (IF, Prem, pSTS, data from left and right hemispheres combined) for these two scanning conditions which revealed that all of these areas were more responsive to biological motion than scrambled motion under both task conditions.