

The role of the extrastriate body area in action perception

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Numerous cortical regions respond to aspects of the human form and its actions. What is the contribution of the extrastriate body area (EBA) to this network? In particular, is the EBA involved in constructing a dynamic representation of observed actions? We scanned 16 participants with fMRI while they viewed two kinds of stimulus sequences. In the *coherent* condition, static frames from a movie of a single, intransitive whole-body action were presented in the correct order. In the *incoherent* condition, a series of frames from multiple actions (involving one actor) were presented. ROI analyses showed that the EBA, unlike area MT+ and the posterior superior temporal sulcus, responded more to the incoherent than to the coherent conditions. Whole brain analyses revealed increased activation to the coherent sequences in parietal and frontal regions that have been implicated in the observation and control of movement. We suggest that the EBA response adapts when succeeding images depict relatively similar postures (coherent condition) compared to relatively different postures (incoherent condition). We propose that the EBA plays a unique role in the perception of action, by representing the static structure, rather than dynamic aspects, of the human form.

INTRODUCTION

One of the most important functions of vision is to provide information about conspecifics—that is, to inform us about the identity, actions, and mental states of other people around us. Extensive research has focused on how the brain extracts this information from the visual input. Converging evidence has accumulated for face-specific brain mechanisms in humans and other primates (Behrmann & Avidan, 2005; Carmel & Bentin, 2002; Desimone, Albright, Gross, & Bruce, 1984; Haxby, Hoffman, & Gobbini, 2002; Kanwisher, 2000). In parallel, other studies have examined the visual analysis of the form and movement of others' bodies. A key observation from this work, which is reviewed briefly below, is that multiple areas of the human brain respond

selectively to some aspect of the human form and its actions.

In the monkey, neurons in the superior temporal sulcus, particularly the anterior portion, are driven by head and body movements (e.g., Jellema & Perrett, 2003; Perrett et al., 1985). In humans, regions of the right posterior STS (pSTS) respond selectively in fMRI to human biological motions, whether depicted in movies (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005), animations (Pelphrey, Mitchell, McKeown, Goldstein, Allison, & McCarthy, 2003), or versions of Johansson's (1973) schematic "point-light walker" displays (Grèzes, Fonlupt, Bertenthal, Delon-Martin, Segebarth, & Decety, 2001; Grossman et al., 2000; see also Allison, Puce, & McCarthy, 2000, for a review). The extrastriate body area (EBA; Downing, Jiang, Shuman, &

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Kanwisher, 2001), located in the posterior inferior temporal sulcus, responds generally and selectively to images of human bodies and body parts (but no more to faces than to objects). Notably this region also responds significantly more to point-light animations than to scrambled controls (Downing et al., 2001; see also Michels, Lappe, & Vaina, 2005; Peelen, Wiggett, and Downing, in press). Finally, a region of the posterior fusiform gyrus responds strongly and selectively to images of the human body without the face (fusiform body area or FBA; Peelen & Downing, 2005a; Schwarzlose, Baker, & Kanwisher, 2005). In this region, the group average activation to bodies (vs. objects) is nearly as strong as that to faces. However, on grounds of a functional dissociation (Peelen & Downing, 2005a; Peelen et al., in press) and high-resolution functional imaging (Schwarzlose et al., 2005) a case has been made for distinct face and body representations in fusiform gyrus. A strong response to point-light displays has also been observed in a similar region (Grossman, Blake, & Kim, 2004; Santi, Servos, Vatikiotis-Bateson, Kuratate, & Munhall, 2003), consistent with activation of the FBA by these schematic stimuli. Finally, the posterior fusiform gyrus shows enhanced activation to emotional, relative to neutral, body postures (Hadjikhani & de Gelder, 2003). This may reflect modulation of FBA activity by attentional or motivational factors.

Action observation, particularly of actions involving interaction with an object, also produces enhanced single-unit activity in the parietal and inferior frontal cortices of monkeys (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Fogassi, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005), and enhanced BOLD activity in similar regions of the human brain (Buccino et al., 2004; Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999). In the monkey, these neurons respond both when the animal makes a particular movement, and when the monkey observes a similar movement. For this reason, these neurons have been termed “mirror neurons” and have been implicated in imitation learning and in the representation of others’ intentions (see Rizzolatti & Craighero, 2004, for a review).

Thus a number of relatively distant cortical areas all respond selectively to some aspect of the visual appearance or actions of other people. An important aim for research on action perception is to distinguish among the functional properties of these regions. The present study moves towards

this goal, by attempting to determine how the EBA contributes to this network of areas. Specifically, we ask whether the EBA is directly involved in representing the dynamic aspects of human actions—that is, in the integration of changes in the configuration of a person’s body over time. This might be expected if the cortical areas reviewed above interact in a mutually reinforcing manner, in which the EBA’s activity is modulated by feedback from the fronto-parietal motor control areas. An account of this sort has been offered (Jeannerod, 2004) to explain the finding that activity in the EBA increases during the (blind) performance of simple visually guided motor movements (Astafiev, Stanley, Shulman, & Corbetta, 2004; Jackson, Meltzoff, & Decety, in press; but see Peelen & Downing, 2005b, for an alternative interpretation). This account could be extended to propose that the EBA receives efferent information about not only executed actions but also (via “mirror” systems) observed actions. Thus, on what we call the “dynamic representation” hypothesis, we would expect the response of the EBA (relative to appropriate controls) to mirror that of the parietal, frontal, and superior temporal regions that respond strongly to (and indeed produce) biological actions.

An alternative—the “static representation” hypothesis—is that the EBA, while playing a role in the perception of others’ bodies, is not directly involved in the dynamic representation of biological actions. Instead, on this account the EBA responds simply to the visual presence of the human form, and is “naive” to higher-level manipulations such as the dynamic context in which the body is viewed (see also Chan, Peelen, & Downing, 2004, for a similar hypothesis). Consistent with the “static representation” hypothesis is a recent model of biological motion perception (Giese & Poggio, 2003). This model, based on computational considerations, neuroimaging studies, and neurophysiological findings, proposes that the EBA’s role is one of representing static “snapshots” of the individual postures that comprise whole-body actions.

How can we distinguish between the static and dynamic representation hypotheses? Much of the neuroimaging research on biological action perception has used point-light animations of simple actions, compared to controls, as experimental stimuli. These stimuli are valuable in that they can test the response of brain regions to biological motion *per se*, in the absence of other visual cues.

However, a limitation of this approach for studying the EBA for the present purposes is that in the experimental condition, one has the percept of a human figure as a result of structure-from-motion. This percept is, by definition, not present in the control conditions typically used. (These include both simple linear or radial motion patterns, and “scrambled” point-light animations, in which individual point movements are retained but the starting points determined randomly.) Thus the differential response to these stimuli in the EBA is ambiguous—perhaps the EBA processes biological motion, but perhaps it simply responds more to the experimental condition because it elicits the percept of a human body. Indeed, previous work has shown that highly schematic depictions of the human body (e.g., silhouettes or stick figures) can selectively activate the EBA (Downing et al., 2001; Peelen & Downing, 2005a).

For this reason, we developed a test of action perception in which the presence of a human figure is constant in both critical conditions. We scanned participants while they viewed two types of displays containing human actors (see Figure 1). The raw materials for both conditions were still frames taken from short movies depicting simple intransitive actions. In the *coherent* condition, the frames were presented in the correct order. In the *incoherent* condition, frames from different movies of one actor were combined to make a single meaningless sequence. In both conditions the displays were presented at a sufficiently slow rate to disrupt the percept of visual motion. Likewise, at this slow rate of presentation the transitions between frames did not give rise to the percept of biomechanically impossible movements (cf. Shiffrar & Freyd, 1990). If the “dynamic representation” account of the EBA is correct, we should expect a greater response to the coherent sequences than to the incoherent sequences, in spite of equivalence in the two conditions at the level of individual frames. In contrast, if the “static representation” hypothesis is correct, we would expect no such difference.

We analyzed the data in two ways. First, we used a functional localizer approach in order to identify the right hemisphere EBA in each participant. For comparison, the right pSTS, FBA, and motion-selective MT+ were also identified. We measured the neural response of each of these regions to the coherent and incoherent sequences. Second, in order to verify that our coherent sequences activated other brain regions

that respond to human actions (e.g., in parietal and frontal cortex), we performed a whole-brain, group-average contrast of coherent and incoherent action sequences.

MATERIALS AND METHODS

Subjects

Sixteen healthy adult volunteers (mean age = 23, range = 18–34; 9 female) were recruited from the University of Wales, Bangor community. Participants satisfied all requirements in volunteer screening and gave informed consent approved by the School of Psychology at the University of Wales, Bangor and the North-West Wales Health Trust. Participation was compensated at £20 per session.

Design and procedure

Localizer scans. Each participant was scanned on a series of blocked-design localizer experiments, in order to identify *a priori* functional regions of interest with respect to individual brain anatomy. One localizer consisted of blocks of images of human faces, human bodies without heads, outdoor scenes, and handheld tools. Each condition was presented in four 15-second blocks within one scan. In each block 20 different images from one category were presented (300 ms on/450 ms off). Each participant was tested with two different versions of the localizer, counterbalancing for the order of the blocks. Participants performed a “1-back” repetition detection task during this localizer. Further details can be found elsewhere (Peelen & Downing, 2005c).

The localizer for area MT+ consisted of low-contrast, concentric rings that either slowly oscillated inwards and outwards, or, in separate blocks, remained static (Tootell et al., 1995). Each condition was presented for eight 15-second blocks. Blocks alternated between moving and static, with a fixation-only block at the beginning and end of the scan, and after every fourth block. The localizer for posterior STS followed a similar design, with 16-second blocks in which either point-light-walker animations or phased-scrambled versions of the same animations were presented (Grossman et al., 2000). Each animation lasted 667 ms, with a 333 ms blank interval between each stimulus.

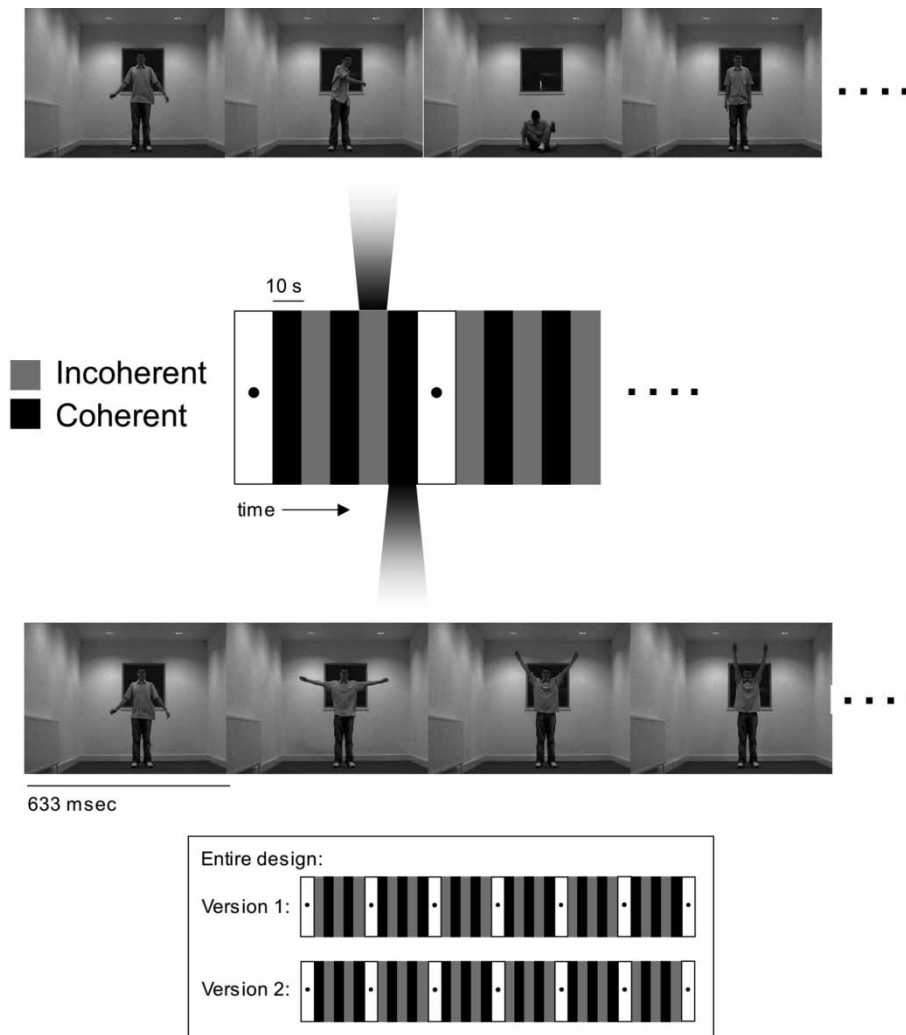


Figure 1. Illustration of the experimental paradigm, with details of the time course of the design and example stimuli.

Main experiment. Each of two actors (1 male, 1 female) were videotaped against a neutral background while performing 15 short actions (e.g., punching, kicking, bending, etc.; see Figure 1 and online Supplementary Materials for examples). The two actors performed different actions. The actors' whole bodies were always visible. None of the actions involved interacting with real objects, although a few of the actions implied interaction with an object (e.g., running a comb through the hair). After the movies were digitized, fifteen individual frames were taken from each action, with each frame separated from the next by approximately 200 ms. These images were used to build the sequences presented in the main experiment.

The design of the main experiment is illustrated in Figure 1. Each participant was scanned

twice, with each scan comprising images of a different actor. There were six major blocks per scan, interrupted by blocks in which only a fixation point was visible for 15 seconds. Each scan also began and ended with a 15-second fixation block. Each of the six major blocks was divided into five minor blocks. In each minor block, coherent and incoherent 15-image sequences were presented in alternation. Half of the major blocks began with a coherent sequence, and half with an incoherent sequence. The initial condition of the run was counterbalanced across scans and participants.

Each image was presented for 633 ms, with no interval between images. The final image of each sequence was followed by a blank screen for 500 ms, resulting in a duration of 10 seconds per sequence. In the coherent blocks, the 15 frames

from a single action were presented in order. In the incoherent blocks, frames from different actions (but always depicting the same actor) were presented. The order of these frames was random, with the constraints that each frame appeared only once per scan, and that no frame was preceded or followed by a frame taken from the same original action movie. Each frame from each action (225 total) appeared exactly once in the coherent condition and once in the incoherent condition in a given scan. Thus the stimuli were matched between the coherent and incoherent conditions at the level of individual images. Participants were told to attend to the sequences but were otherwise given no explicit task.

Data acquisition

A 1.5T Philips MRI scanner with a SENSE parallel head coil was used. For functional imaging, a single-shot EPI sequence was used (T2* weighted, gradient echo sequence, TE = 50 ms, flip angle 90°). Localizers were scanned with TR = 3000 ms, 20–22 off-axial slices with no gap, voxel dimensions of 3.75 × 3.75 × 5 mm ($N = 10$) or 3 × 3 × 4 mm ($N = 6$). The main experiment was scanned with TR = 3000 ms, 22 slices with no gap, 3.75 × 3.75 × 5 mm voxel dimensions, except for one participant (20 slices at 3 × 3 × 4 mm).

Data analysis

Pre-processing and statistical analysis of MRI data was performed using BrainVoyager 4.9 (Brain Innovation, Maastricht, The Netherlands). Three dummy volumes were acquired before each scan in order to reduce possible effects of T1 saturation. Functional data were motion-corrected, low-frequency drifts were removed with a temporal high-pass filter (0.006 Hz), and spatial smoothing was applied with a 6 mm FWHM filter. Functional data were manually co-registered with 3D anatomical T1 scans (1 × 1 × 1.3 mm resolution, resampled to 1 × 1 × 1 mm voxels with trilinear interpolation). The 3D anatomical scans were transformed into Talairach space (Talairach & Tournoux, 1988), and the parameters for this transformation were subsequently applied to the co-registered functional data, which were resampled to 1 × 1 × 1 mm voxels.

For each participant, general linear models were created for each localizer experiment and for the main experiment. One “boxcar” predictor (convolved with a standard model of the HRF) modeled each condition. Regressors were also included to account for differences in global signal across scans.

In each participant, the localizer scans were used to define the EBA by contrasting the response to human bodies with that to the average of faces, tools, and scenes. The FBA was defined by contrasting bodies against tools. We identified area MT+ by contrasting the response to moving concentric rings with that to static rings. Finally, the posterior STS ROI was identified by comparing the response to point-light walker stimuli with phase-scrambled versions of the same stimuli. Analyses were restricted to right hemisphere ROIs, on the basis of evidence that the EBA, FBA, and pSTS biological motion regions are weaker or non-existent in the left hemisphere (Downing et al., 2001; Peelen & Downing, 2005a, 2005c; Allison et al., 2000).

For each ROI in each subject, the most significantly activated voxel was identified within a restricted part of cortex based on previously reported anatomical locations (EBA: Peelen & Downing, 2005c; FBA: Peelen & Downing, 2005a; MT+: Dumoulin et al., 2000; pSTS: Grossman et al., 2000). ROIs were defined as the set of contiguous voxels that were significantly activated (all $p < .0001$ uncorrected, except pSTS: $p < .005$) within a 9 mm cube surrounding the peak voxel. This procedure was adopted for four reasons: (1) to ensure that regions were defined objectively; (2) to ensure that they were segregated from nearby selective activations; (3) to roughly equate the number of voxels included across different regions of interest; and (4) to ensure that only the most selective voxels were included in the ROI. Within each ROI in each subject, a further general linear model was then applied, modeling the response of the voxels in the region, in aggregate, to the coherent and incoherent conditions of the primary experiment. The regression weights from this GLM provided the basis for the ROI results described below.

Finally, a whole-brain, group average analysis was conducted on data from the main experiment. Fixed-effects contrasts were performed, at an uncorrected threshold of $p < .000005$, to test for regions more active in either the coherent or incoherent conditions. Only clusters $> 100 \text{ mm}^3$ are reported for this analysis.

RESULTS

ROI analyses. We successfully identified the right hemisphere ROIs in all participants, with the exception of pSTS, which was identified in 15/16 participants. The mean (with SEM) Talairach co-ordinates of the ROI peaks were as follows: EBA: 48 (1.3), -70 (1.5), 0 (1.5); pSTS: 54 (1.6), -46 (1.9), 12 (1.8); MT+: 44 (1.1), -67 (1.7), -3 (1.8); FBA: 41 (0.7), -43 (2.1), -19 (1.4). Further ROI analyses were conducted on the 15 participants who showed all ROIs.

Average parameter estimates for each ROI are given in Figure 2. An initial 2 (coherent or incoherent) $\times 4$ (EBA, pSTS, MT+, or FBA) within-subjects ANOVA showed a significant main effect of ROI, $F(3, 42) = 7.4$, $p < .001$, and, more important, a significant interaction of ROI with coherence, $F(3, 42) = 6.2$, $p < .005$. The main comparisons of interest for the ROI analyses concerned whether the EBA showed similar or different effects of coherence as compared to pSTS, MT+, and FBA. Therefore we performed a 2×2 within-subjects ANOVA comparing the effects of coherence in the EBA and each of these regions. The comparison of the EBA and pSTS revealed a significant interaction, $F(1, 14) = 15.7$, $p < .001$, and a main effect of ROI, $F(1, 14) = 11.7$, $p < .005$. Follow-up t -tests showed that in the EBA, there was a significantly greater response to incoherent than to coherent sequences, $t(14) = 3.0$, $p < .01$. In pSTS, in contrast, the response was marginally greater to coherent than to incoherent sequences, $t(14) = 1.8$, $p < .1$. Area MT+ and the

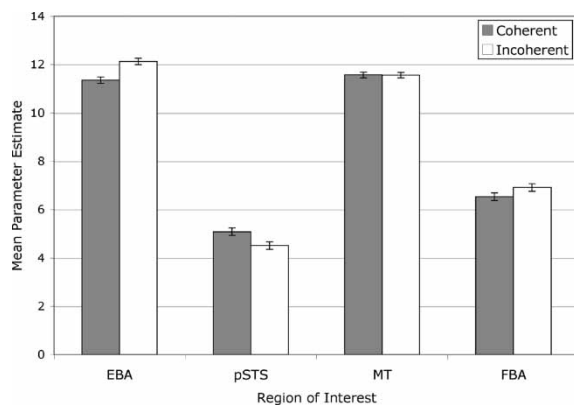


Figure 2. Results of the region of interest analysis. Mean parameter estimates are given for the response to coherent and incoherent sequences, in the right hemisphere extrastriate body area, posterior superior temporal sulcus, area MT+, and fusiform body area. Error bars reflect within-subjects standard error of the mean calculated for each ROI separately.

EBA also showed significantly different effects of coherence, $F(1, 14) = 12.6$, $p < .005$. A simple effects test revealed no effect of coherence in MT+, $t(14) = 0.03$, *ns*. Finally, the EBA and FBA showed a significant main effect of coherence, $F(1, 14) = 6.2$, $p < .05$, but no interaction, $F(1, 14) = 1.3$, $p = .28$. A simple effects test in the FBA alone showed no significant effect of coherence, $t(14) = 1.1$, *ns*. (The response of the FBA interacted significantly with pSTS, $F(1, 14) = 8.5$, $p < .025$, but not with MT+, $F(1, 14) = 1.1$, $p = .30$.) In sum, in the EBA, incoherent sequences produced a larger response than coherent sequences. This pattern was reliably different from that observed in pSTS and MT+, but not FBA.

Whole-brain analyses. The whole brain analysis was conducted on the data from all 16 participants. We observed significant increases to the coherent condition, relative to the incoherent condition, in the right parietal cortex, right ventral inferior frontal gyrus, and left occipitotemporal cortex (see Figure 3). A list of all activations greater than 100 mm^3 in extent is given in Table 1.

We found no significant clusters greater than 100 mm^3 that responded more to incoherent than to coherent sequences. In an exploratory analysis, the contrast was repeated at a threshold of $p < .005$ uncorrected. Activations were observed in several regions, including right orbitofrontal and superior frontal areas, medial prefrontal cortex, right occipital and occipitotemporal cortex, and right inferior occipitotemporal cortex (Table 2). Given the absence of any coherence effect in the independently localized MT (see above), we attribute the increased activity to the incoherent sequences seen in early visual cortex to a greater amount of high-contrast visual transients, relative to the coherent condition. The peak co-ordinates of the right occipitotemporal region ($45, -73, -1$) were similar to those found in the EBA localizer ($48, -70, 0$). To explore this similarity further, we extracted the response of this region, as defined in the group-average incoherent vs. coherent contrast, to each of the four stimulus categories tested in the EBA localizer experiment (bodies, faces, tools, and scenes). A one-way ANOVA on these values showed a significant effect of category, $F(3, 45) = 9.0$, $p < .001$. The mean response to bodies ($M = 6.9$) was greater than to scenes ($M = 3.2$), faces ($M = 4.0$), and tools ($M = 4.4$), all $t(15) > 3.2$,

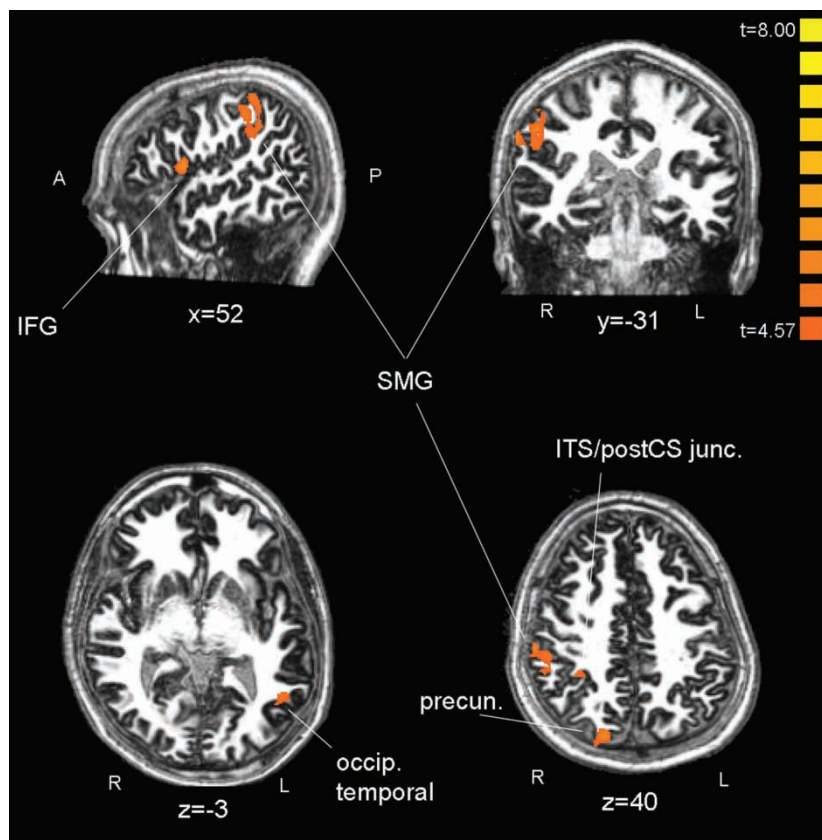


Figure 3. Activations from the whole-brain analysis. Colored regions are those that responded more to coherent than to incoherent sequences, in a whole-brain, fixed-effects group average analysis. For clarity these regions are overlaid on an anatomical scan from a single participant. Activations are thresholded at $p < .000005$, uncorrected. Only activations greater than 100 mm^3 are shown. See Table 1 for details.

all $ps < .01$. Thus the preference for incoherent over coherent sequences in the right EBA (defined in individual ROIs) is sufficiently strong and consistent to be observed at the group-average level, albeit at a liberal statistical threshold. Additionally, this preference does not appear to spread extensively within extrastriate cortex.

DISCUSSION

Our aim for this study was to distinguish two hypotheses about the functional role of the EBA within the network of cortical areas that analyze the human form and its characteristic motions. We found that, in contrast to both pSTS and

TABLE 1

All activations for which coherent > incoherent, from a fixed-effects multiple regression analysis, thresholded at $T > 4.57$, $p < .000005$ uncorrected. Only activations above a minimum spatial extent of 100 mm^3 are shown. Each row gives the location of the cluster, the volume of the activation, the location of the peak voxel of that activation in Talairach co-ordinates, the maximum and mean T value for the region, and the associated p value for the region as a whole

Region	Extent (mm^3)	Mean peak			Maximum (T)	Mean (T)	Mean (p)
		X	Y	Z			
R supramarginal gyrus	2187	56	-31	35	6.1	4.92	.000002
R dorsal precuneus	1061	19	-75	41	6.27	4.96	.000002
R IPS/postcentral junction	833	37	-44	51	5.71	4.93	.000002
R ventral inferior frontal gyrus	427	52	8	7	6.22	5.08	.000001
L ventral occipitotemporal	119	-50	-58	-4	5.34	4.79	.000002

TABLE 2

All activations for which incoherent > coherent, from a fixed-effects multiple regression analysis, thresholded at $T > 2.81$, $p < .005$ uncorrected. (There were no significant activations for this contrast at the threshold of $T > 4.57$ reported in Table 1.) Only activations above a minimum spatial extent of 100 mm^3 are shown. Each row gives the location of the cluster, the volume of the activation, the location of the peak voxel of that activation in Talairach co-ordinates, the maximum and mean T value for the region, and the associated p value for the region as a whole

Region	Extent (mm^3)	Mean peak			Maximum (T)	Mean (T)	Mean (p)
		X	Y	Z			
L posterior occipital lobe	1324	-12	-96	-1	5.01	3.40	.0014
R angular gyrus	631	47	-66	32	3.64	3.08	.0024
R inferior occipitotemporal	390	45	-73	-1	3.67	3.06	.0026
R posterior occipital lobe	380	14	-94	7	5.18	3.60	.0010
R orbitofrontal cortex	341	17	42	-1	4.69	3.36	.0020
R medial prefrontal	242	1	38	23	3.49	3.00	.0030
R superior frontal gyrus	107	19	18	54	3.74	3.19	.0020

MT+ (localized in individual subjects), and frontal and parietal regions (identified in a whole-brain analysis), the right EBA responds significantly more to incoherent action sequences than to coherent sequences. This preference is particularly striking given previous evidence for an enhanced EBA response to point-light biological actions relative to scrambled controls (Downing et al., 2001; Grossman et al., 2002; Peelen et al., in press). Our findings are inconsistent with the “dynamic representation” hypothesis. They indicate that the EBA’s functional contribution to the perception of human action is distinct from that of the other relevant areas involved in action perception.

The EBA did not respond more to coherent than to incoherent sequences; in fact it showed a significant bias in the opposite direction. One possibility is that this is due to the presence of more motion in the transition between frames in that condition, compared to the coherent condition. This seems unlikely given that motion-selective area MT+ showed essentially identical responses to the coherent and incoherent sequences, a significantly different pattern from that seen in the EBA. We instead propose that the EBA effect represents a form of neural adaptation. Several studies have found reduced responses in visual cortex to repeated or “primed” stimuli, compared to previously unseen stimuli (e.g., Buckner et al., 1998). This effect has been used as a tool to reveal the functional properties of cortical areas, by assessing the kinds of stimulus changes to which the adaptation effect (and presumably the neurons under investigation) are invariant (e.g., Grill-Spector & Malach, 2001; Kourtzi & Kanwisher, 2001; Vuilleumier, Henson,

Driver, & Dolan, 2002). In the coherent condition of the present study, the configuration of the actor’s limbs changed relatively little, on average, from frame to frame (see Figure 1). A region that processes the *static* visual appearance¹ of the human figure would be expected to respond less in this situation, due to the similarity between succeeding stimuli, compared to a situation in which the configuration changed much more dramatically from frame to frame. This effect was not predicted for the EBA, so this account is necessarily post hoc, and requires further tests. An open question is whether this region also processes the static structure of non-body object kinds. If this were the case, one would expect a similar effect of coherence for these other object kinds. However, this seems unlikely owing to (a) the weak response to other categories in EBA (Downing et al., 2001, in press) and (b) the finding that TMS over the EBA selectively impairs visual short term memory for bodies (Urgesi et al., 2004).

In common with previous studies of fMRI adaptation effects (see Henson, 2003, for a review), it is difficult to distinguish between an account in which neural activity is suppressed when identical or similar stimuli are perceived, and one in which activity is enhanced due to the novelty of changing stimuli. Likewise the effects of repetition on attentional state and neuronal adaptation can be difficult to disentangle. We

¹ Here we emphasize the EBA’s sensitivity to changes in *configuration*, i.e., gross changes in the arrangement of the limbs relative to each other. We do not test the additional possibility that the EBA also represents the *form* of the body, e.g., differences in the contour and texture of body parts (cf. Urgesi, Berlucchi, & Aglioti, 2004).

note, however, that in the present study the reduced EBA activity to coherent sequences is unlikely to be due to global changes in arousal, given that on the whole, across the whole brain far more neural activity was elicited by the coherent relative to the incoherent sequences.

A secondary finding from the ROI analyses was that while the FBA did not significantly distinguish coherent from incoherent sequences, its response was similar to that found in the EBA (and this pattern significantly interacted with pSTS). Tentatively, we group the FBA, in terms of its functional properties, with EBA rather than pSTS. This raises the possibility that the observed adaptation effect originates in one of the two body-selective areas and is transmitted to the other (cf. Tolia, Keliris, Smirnakis, & Logothetis, 2005). A key question for further studies is how the EBA and FBA interact. High temporal-resolution sampling could be used to test whether the functional connectivity between these regions is directionally biased. Additionally, manipulations of tasks and or stimuli could be tested in order to determine whether the EBA and FBA are functionally dissociable.

Finally, the whole-brain analyses confirmed, at the group level, the preference for incoherent sequences in the EBA (at a liberal statistical threshold). In contrast, several regions were activated more by coherent than incoherent sequences (see Figure 3 and Table 1). Some of these regions have been identified in previous neuroimaging studies of action observation. A classic study measuring brain responses to finger movements and to observation of similar movements (Iacoboni et al., 1999) found activity common to both tasks in the left frontal operculum (peak Talairach co-ordinates: $-50, 12, 12$) and at the junction of the right hemisphere intraparietal sulcus with the postcentral sulcus (peak: $37, -40, 57$). We find similar activations, except that in the present study the frontal operculum activation is in the right hemisphere (operculum: $52, 8, 7$; IPS/PostCS: $37, -44, 51$). Activations in these areas were also found in a recent fMRI study in which expert ballet and capoeira dancers observed movies of both ballet and capoeira dance moves (Calvo-Merino et al., 2005). Effects of expertise (i.e., differential effects of observation for familiar vs. unfamiliar actions) were found in the two regions mentioned above, as well as in the right supramarginal gyrus (peak MNI co-ordinates: $57, -30, 48$), in line with the

present findings (Talairach peak: $56, -31, 35$). Thus our whole brain results support two main conclusions: (1) the coherent action sequences used as stimuli here activate areas that are known to be implicated in action observation, even though the motion signals typically present when viewing actions were absent; and (2) the EBA, as indicated by its preference for incoherent sequences, plays a different functional role than these other areas.

To summarize, we speculate that the EBA computes a static representation of the human body, and is not involved in analysis of biological motion *per se*. This is a somewhat paradoxical finding, in view of the EBA's enhanced response to intact vs. scrambled point-light animations (Downing et al., 2001; Grossman & Blake, 2002). This is in contrast to pSTS, which is strongly engaged by point-light animations, and weakly selective for coherent actions when the low-level biological motion signals are removed. These findings are consistent with a recent computational model of biological motion processing (Giese & Poggio, 2003). In this model, subregions within a form-selective pathway (including the EBA) combine with separate motion-selective analyzers to learn to recognize biological actions. The model proposes a set of "snapshot" neurons in the ventral stream that represent the various static postures that comprise an action. The present findings suggest that the EBA contributes to this function, thus performing a fundamental step in our visual representation of the behavior of other individuals.

These results provoke a number of questions for further research. First, it would be valuable to compare a wider variety of types of actions, particularly object-directed actions and semantically meaningful actions. Second, manipulations of subjects' tasks (e.g., in which the action itself is either task relevant or irrelevant) have previously been found to alter the brain activity elicited by viewing actions (e.g., Decety et al., 1997). Whether this would also modulate EBA activity is an open question, although the framework proposed here would predict no such effect, provided other factors such as attentional engagement were controlled. Finally, disruptive techniques could test the proposal that the EBA provides a crucial initial step in biological motion perception. Specifically, we predict that disruption of EBA activity by transcranial magnetic stimulation (TMS) would result in subsequent abnormal neural responses to biological motion

in posterior superior temporal sulcus and frontoparietal action systems.

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