fMRI analysis of body and body part representations in the extrastriate and fusiform body areas

John C. Taylor, Alison J. Wiggett, Paul E. Downing
School of Psychology
University of Wales, Bangor
United Kingdom

Running head: Body processing in EBA and FBA

Correspondence to:
Paul Downing
School of Psychology
Adeilad Brigantia
Penrallt Road
Bangor, UK LL57 2AS
p.downing@bangor.ac.uk

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Abstract

This study examined the contributions of two previously-identified brain regions -- the extrastriate and fusiform body areas (EBA and FBA) -- to the visual representation of the human form. Specifically we measured in these two areas the magnitude of fMRI response as a function of the amount of the human figure that is visible in the image, in the range from a single finger to the entire body. A second experiment determined the selectivity of these regions for body and body part stimuli relative to closely-matched control images. We found a gradual increase in the selectivity of the EBA as a function of the amount of body shown. In contrast, the FBA shows a step like function, with no significant selectivity for individual fingers or hands. In a third experiment we demonstrate that the response pattern seen in EBA does not extend to adjacent motion-selective area hMT. We propose an interpretation of these results by analogy to nearby face-selective regions OFA (occipital face area) and FFA (fusiform face area). Specifically, we hypothesize that the EBA analyzes bodies at the level of parts (as has been proposed for faces in the OFA), whereas FBA (by analogy to FFA) may have a role in processing the configuration of body parts into wholes.
Introduction

The ability to identify and interpret the actions and intentions of other people is a crucial human social skill. Accurate perception of the human body and its individual parts can be seen as a necessary component of this broader task. Functional magnetic resonance imaging (fMRI) studies have previously identified two regions of extrastriate visual cortex that are highly sensitive to visual depictions of the human body, relative to non-body control objects. These regions have been designated the extrastriate and fusiform body areas -- EBA (Downing et al., 2001, 2006a,b, 2007; Peelen and Downing 2005c) and FBA (Peelen and Downing, 2005b; Peelen et al., 2006; Schwarzlose et al., 2005) respectively. The EBA is found at the posterior end of the inferior temporal sulcus, and the FBA is found in the lateral posterior fusiform gyrus (see Fig. 1). Although these two areas are thought to contribute to the perception of bodies and/or body parts, to date there is no evidence on whether and how they might be functionally distinguished.

A possible basis for understanding the relative functional contributions of the EBA and FBA to body perception comes from our understanding of face processing. There are several reasons to think the cortical systems that analyse bodies and faces might be similar. Most obviously, bodies and faces are nearly always perceived together in space and time – seeing a body without the face or vice versa is rare. Second, both stimuli are biologically relevant and carry important information about conspecifics, such as their gender, actions, and intentions. Finally, inversion of both faces and bodies interferes with their identification, relative to other object kinds (Reed et al., 2003; Yin, 1969).
The functional neuroanatomy of face and body processing are also similar in some ways. In the macaque, fMRI studies have identified adjacent or overlapping face- and body-selective regions of superior temporal sulcus (Tsao et al., 2003; Pinsk et al., 2005). In humans, two ventral occipitotemporal areas respond selectively to faces, relative to scenes and non-face objects (see Figure 1): the occipital face area (OFA; Puce et al., 1996; Kanwisher et al., 1997; Rossion et al., 2003), which is found on the ventral surface of the occipital lobe, and the fusiform face area (FFA; Kanwisher et al., 1997), which is found on the lateral fusiform gyrus, where it closely overlaps the FBA (Peelen and Downing, 2005b; Peelen et al., 2006; Schwarzlose et al., 2005).

An influential model of face processing (Haxby et al., 2000) proposes (in part) a hierarchical scheme in which the OFA analyses individual facial features, superior temporal sulcus analyses facial expressions and lip movements, and the FFA analyses the invariant, identity-related aspects of the face (but see Calder and Young, 2005; Schlitz and Rossion, 2006, for challenges to this scheme). The latter of these functions requires configural processing of the features of the face, i.e. consideration of their mutual spatial relationships. Consistent with this model, for example, is the finding that the FFA’s response to facial features is weakened by disrupting their normal configuration, but not by replacing them with simple geometric shapes -- whereas in the OFA configuration has no effect, but the photorealism of the individual face features is important (Liu et al., 2003).

Here we take as a starting point an analogy between OFA and EBA, and between FBA and FFA, in terms of their functional properties. If OFA / EBA and FFA / FBA share functional properties, EBA and FBA may be distinguishable in terms of their
Body processing in EBA and FBA responses to bodies and body parts. Specifically, we hypothesized that the EBA consists of a population of neurons whose driving features consist primarily of parts of the body, whereas the neurons comprising FBA are more responsive to the visual appearance of the whole body (or larger segments of the body).

To test this hypothesis, in two experiments we used block-design fMRI paradigms to measure the EBA and FBA activity elicited by body parts ranging from a single digit to the entire body (sans head). We functionally localised these ROIs in each subject individually with a balanced combination of two contrasts: whole (headless) bodies vs chairs, and body parts vs assorted object parts. This procedure avoids biasing the selection of voxels towards whole- or part-based selectivity. In the first experiment, we measured the mean response of the EBA and FBA to fingers, hands, arms, and torsos (see sample stimuli in Figure 2), while subjects performed a 1-back memory task. In the second experiment, we used a similar design to compare bodies and body parts to closely-matched trees/tree parts (see sample stimuli in Figure 3) to test whether the effects of hierarchical level are specific to human bodies, or instead reflect a more general process that applies to other object kinds. In a third experiment we replicated Experiment 2 in an event-related paradigm, with the addition of an independent localiser for human motion-selective area hMT. This allowed us to test whether our EBA results could alternatively be explained by activation in hMT, which overlaps closely with the EBA (Downing et al., 2001, 2007; Peelen et al., 2006).
**Experiment 1**

*Materials and methods*

**Participants.** Ten healthy, adult volunteers (3 male) were recruited from within the University of Wales, Bangor community. All participants were fully briefed and informed consent was obtained in compliance with procedures set by the School of Psychology ethics panel and the North West Wales Health Trust.

**Stimuli and Apparatus.** All data were acquired using a 1.5T Philips Intera ‘Compact Plus’ MRI scanner, fitted with a SENSE parallel head coil (Philips, Best, The Netherlands). Stimulus images were presented using a Sanyo LCD projector (Sanyo, Osaka, Japan) focused onto a translucent rear-projection screen. Presentation was controlled using MatLab (Mathworks, Natick, MA) Psychophysics Toolbox (Brainard, 1997; Pelli, 1997), running on an Apple iBook G3 laptop computer with Macintosh OS9 operating system (Apple, Cupertino, CA). 1-back responses were recorded using a non-ferrous, fibre optic response pad (Current Designs, Philadelphia, PA). Pre-processing and statistical analysis were performed using BrainVoyager 4.9 software (Brain Innovation, Maastricht, The Netherlands).

Stimuli for the main experiment were 16 images each of human body parts, comprising: headless human torsos in a variety of natural postures, arms (including hands and fingers), hands (including fingers) and fingers (see Fig. 2). All stimuli were greyscale and were normalised to 400 x 400 pixels on a ‘netscape’ grey background (192R, 192G, 192B). For one localiser experiment, the stimuli comprised 20 images of headless human bodies in a variety of postures; these were compared to 20 different
chairs as a control. A second localiser experiment compared a variety of body parts with a variety of parts of common objects. To reduce the risk of over-familiarising subjects with the stimuli, the body and body part images used for the localiser blocks were different from those used in the main experiment. Participant attention was maintained and monitored during all localiser and experimental runs using a 1-back task (two randomly-placed instances per block). Image positions were jittered slightly on alternate presentations to prevent reliance on low-level transient detection.

**Scanning parameters.** Functional data were obtained using T2* weighted scans employing a single shot echo planar (EPI) sequence. Twenty axial oblique slices were scanned to include, bilaterally, the frontal and prefrontal areas, and temporal and occipital lobes (including the fusiform gyrus). Acquisition parameters for all participants were: 64 x 64 matrix, slice thickness = 4 mm, voxel dimensions = 3 mm x 3 mm in-plane; echo time (TE) = 50 ms; repetition time (TR) = 2000 ms; flip angle = 90°. Parameters for T1 weighted anatomical scans were: 256 x 256 matrix; slice thickness = 1.3 mm; voxel dimensions = 1 x 1 mm in-plane; TR = 12 ms, TE = 3 ms; flip angle = 8°.

**Localisers.** ROIs were localised individually in two separate runs, one comparing bodies to chairs and the other comparing body parts to object parts. EBA was localised bilaterally. Only right hemisphere FBA was examined because significant body-selective activity in the left fusiform gyrus is rare. Each localiser run consisted of twenty-one 15-second blocks. Blocks 1, 6, 11, 16, and 21 were fixation-only baseline epochs. In each of the remaining blocks, 20 images of either headless human bodies and images of chairs, or human body parts and parts of common non-natural objects were presented. Stimuli were each displayed for 300 ms, followed by a blank screen for 450 ms.
Main experiment. Participants were scanned on two blocked-design runs. Each run consisted of twenty-one 16-second blocks. Blocks 1, 6, 11, 16, and 21 were fixation-only baseline epochs. The remaining 16 blocks each comprised 16 images each, presented serially. Each image was displayed for 300 ms followed by a 700 ms blank interval. Each sequence comprised four blocks of body related stimuli (torso, arm, hand or finger). Block orders within each sequence and the presentation order of items within each block were fully counterbalanced across experimental runs such that the mean serial position of each condition was equalised across participants. 168 functional data volumes were acquired for each experimental scan.

Data pre-processing. 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). No spatial smoothing was applied. Functional data were manually co-registered with 3D anatomical T1 scans (1 x 1 x 1.3 mm resolution). The 3D anatomical scans were transformed into Talairach space (Talairach and Tournoux, 1988), and the parameters from this transformation were subsequently applied to the co-registered functional data.

ROI Analyses. For each participant, general linear models (GLMs) were created for the localisers and the main experiment. One boxcar predictor, convolved with a delayed gamma function (delta = 2.5 s; tau = 1.25 s) to model the hemodynamic response (Boynton et al., 1996), modelled each condition of interest. Regressors of no interest were also included to account for differences in the mean MR signal across scans. Regressors were fitted to the MR timeseries in each voxel and the resulting beta
parameter estimates were used to estimate the magnitude of response to each experimental condition.

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 (Peelen and Downing, 2005a,b). The ROIs were defined by [bodies+body parts] – [chairs+object parts]. Each ROI was defined by its “peak” voxel and all voxels within a 9 mm cube centred on the peak that met an uncorrected statistical threshold of $p < 0.0001$. These voxels were then submitted to a further ROI-GLM analysis of the data from the main experiment. The betas from these regression analyses provided estimates of the response to the experimental conditions, which were subsequently analysed with ANOVAs. Polynomial and difference contrast metrics were then calculated from ROI data by comparing factor levels for each stimulus category as follows: level 1 (finger); level 2 (hand); level 3 (arm); level 4 (torso).

**Results**

The left and right EBA, and right FBA, were successfully identified in all 10 subjects. The mean spatial coordinates (with standard errors) of these regions, in Talairach space, were: left EBA: X: -47.4(1.4), Y: -71.2(1.3), Z: 0.1(1.7); right EBA: X: 48.5(1.8), Y: -65.2(1.7), Z: 3.5(1.5); FBA: X: 38(1.3), Y: -41.2(1.6), Z: -17(1.5).

The response pattern from the three ROIs is illustrated in Figure 2. Comparing right vs. left EBA, a repeated measures ANOVA (hemisphere x level) revealed a significant main effect of level $F (1, 9) = 50.79, p < .001$; but no main effect of
hemisphere ($p > 0.05$). The interaction of hemisphere x level approached significance, $F(3, 27) = 3.01, p = .081$ (Greenhouse - Geisser correction applied). Given the near-significant interaction in the comparison of left and right EBA, it was deemed inappropriate to collapse these ROIs into a single variable. For this reason we report separate comparisons of left and right EBA, each against right FBA.

For the comparison of right EBA and right FBA, main effects of both ROI and level were significant, $F(1, 9) = 6.14, p = .04$ and $F(3, 27) = 28.55, p < .001$ respectively. The interaction of ROI x level approached significance, $F(3, 27) = 3.79, p = .053$ (Greenhouse - Geisser correction applied). For the comparison of left EBA and right FBA, the main effect of level was again significant, $F(1, 9) = 23.18, p < .001$, and there was no main effect of ROI ($p > 0.05$). The interaction of ROI x level approached significance $F(3, 27) = 3.52, p = .064$ (Greenhouse - Geisser correction applied).

**Contrast Analysis.** The specific predictions of the hypothesis regarding the responses to body parts were examined using difference and polynomial contrasts in each ROI. In right EBA, all difference contrasts [weights on each level of stimulus hierarchy, for finger, hand, arm, and torso: (-1, +1, 0, 0), (-1, -1, +2, 0), and (-1, -1, -1, +3)] were significant $F(1, 9) = 6.93, p = .027$; $36.62, p < .001$; and $42.76, p < .001$, respectively. This was also the case in left EBA ($F(1, 9) = 10.26, p < .01$; $38.67, p < .001$; and $34.21, p < .001$). In FBA the contrasts (-1, +1, 0, 0) and (-1, -1, +2, 0) were not significant, but the remaining comparison (-1, -1, -1, +3) was significant: $F(1, 9) = 17.09, p = .003$.

Polynomial contrasts revealed significant linear effects in all ROIs, right EBA: $F(1, 9) = 47.13, p < .001$; left EBA, $F(1, 9) = 45.59, p < .001$; FBA, $F(1, 9) = 16.95, p = .003$. 
Significant quadratic effects were found in the FBA and right EBA, $F(1, 9) = 7.94, p = .02$ and $F(1, 9) = 4.98, p = 0.05$, respectively.

**Discussion**

The results of Experiment 1 show how the EBA and FBA differ in their response to body part images of varying completeness. Notably, in the left and right EBA the response to body parts rose gradually as more of the body hierarchy was visible. In contrast, the response in the FBA to fingers, hands, and arms, though non-zero, was relatively constant. A step-like increase in response was elicited when whole torsos were presented. These findings hint at a distinction between left and right EBA, though the difference in response pattern between these ROIs appears to lie more in the steepness of the change in response as a function of level, rather than in a qualitative difference. More important for the present purposes, they provide new evidence for a distinction between the functional characteristics of the EBA and FBA.

In a second experiment, we compared body parts from varying hierarchical levels to closely-matched tree parts presented at similar levels (see bottom of charts in Figure 3). Specifically, fingers were matched to single leaves; hands were matched to leaf clusters; arms were matched to branches; and bodies were matched to trees. The inclusion of this control condition allowed us to test whether the effects of hierarchical level observed in Experiment 1 are specific to human bodies or instead reflect a more general process that applies to other object kinds.
Experiment 2

Materials, Methods, Design and Procedure

With the following exceptions, all procedures were identical to those reported in Experiment 1. We tested 20 participants with stimuli from eight conditions derived from a 2 (category: body, tree) x 4 (hierarchical level) factorial design. The design of the main experiment was as in Experiment 1, except that in each scan stimuli from each of the eight conditions appeared twice, in two separate blocks. Contrast analyses were extended to include tree stimuli: level 1 (finger / leaf), level 2 (hand / cluster), level 3 (arm / branch), level 4 (body / tree).

Results

Localisers. Data from three participants were excluded from analysis due to scanner failure during localiser runs. A fourth data set was excluded on the basis of 1-back data indicating low attention to the stimuli (< 50% of targets correctly identified). The EBA was identified, bilaterally, in all 16 remaining subjects. The right FBA was successfully localised in 15 of the 16 participants, although a more lenient voxel selection threshold ($p < .005$) was required in two cases.

The mean spatial coordinates (with standard errors) of these regions, in Talairach space, were: left EBA: X: -44 (1.1), Y: -70 (1.3), Z: 2 (1.7); right EBA: X: 52 (0.8), Y: -64 (0.9), Z: 4 (2.0); and FBA: X: 41 (1.3), Y: -44 (1.2), Z: -14 (1.9). To allow consideration of the full factorial design, the analyses were restricted to data from the 15 participants for whom all ROIs could be localised.
Main experiment. Mean responses, with associated standard errors, for each condition in each ROI are presented in Figure 3. A 2 x 2 x 4, repeated measures ANOVA (ROI x category x hierarchical level) comparing left and right EBA revealed significant main effects of hemisphere (left > right) \( F(1, 14) = 7.49, p = .016 \); category \( F(1,14) = 164.48, p < .001 \); and level \( F(3, 42) = 23.70, p < .001 \) (Huynh-Feldt correction applied). The interaction of category x level was significant \( F(3, 42) = 20.45 p < .001 \) but all other two and three-way interactions were not significant. Following Experiment 1, left and right EBA were compared separately with right FBA. An analysis comparing left EBA and right FBA showed significant main effects of ROI, \( F(1, 14) = 4.93, p = .043 \); category \( F(1, 14) = 162.36, p < .001 \); and level \( F(3, 42) = 30.25, p <.001 \). Significant interactions of ROI x category and category x level were also found, \( F(3,42) = 7.48, p <.001 \) and \( 16.02, p <.001 \), respectively. The three-way interaction (ROI x category x level) was not significant. For the comparison of right EBA and right FBA, significant main effects were found for category (bodies > trees) \( F(1,14) = 75.54, p < .001 \); and level \( F(3, 42) = 27.93, p < .001 \). Critically, the three-way interaction of ROI x category x level was significant, \( F(3, 42) = 3.02, p = .04 \).

Follow-up analyses were conducted on each ROI separately, in the form of separate 2 x 4 ANOVAs of category x level. In the right EBA, the main effects of category and level were significant: \( F(1, 14) = 80.26, p < .001 \) and \( F(3, 42) = 16.37, p < .001 \), respectively. The interaction of category x level was also significant: \( F(3, 42) = 15.42, p < .001 \) (Greenhouse - Geisser correction applied). Follow-up t-tests of the effect of category revealed significantly greater responses to body than to tree images at all four
hierarchical levels: $t(14) = 5.69, p < .001; t(14) = 7.33, p < .001; t(14) = 8.26, p < .001; t(14) = 6.79, p < .001$, levels 1 (hands/leaves) to 4 (bodies/trees) respectively.

In the left EBA, main effects of category and level were also significant: $F(1,14) = 211.64, p < .001$ and $F(3, 42) = 21.56, p < .001$ as was the interaction of category x level $F(3, 42) = 16.26, p < .001$. Post-hoc t-tests again showed the same pattern as the right hemisphere: $t(14) = 10.62, p < .001; t(14) = 10.39, p < .001; t(14) = 13.96, p < .001$ and $t(14) = 8.44, p < .001$, for comparisons at levels 1 (hands/leaves) to 4 (bodies/trees) respectively.

In the FBA, the main effects of category and level were significant: $F(1, 14) = 26.53, p < .001$ and $F(3, 42) = 23.72, p < .001$, respectively. The interaction of category x level was also significant: $F(3, 42) = 9.01, p < .001$ (Greenhouse - Geisser correction applied). In contrast to the EBA, significant category selectivity was observed only for the third and fourth hierarchical levels (branches vs. arms; trees vs. bodies): $t(14) = 1.66, p = .12; t(14) = 1.53, p = .15; t(14) = 8.92, p < .001; t(14) = 6.19, p < .001$, levels 1 (hands/leaves) to 4 (bodies/trees) respectively.

**Contrast Analysis.** The specific predictions of the hypothesis regarding the shape of the response profiles to bodies and trees were examined using difference and polynomial contrasts in each ROI. In the right EBA, all difference contrasts (-1, +1, 0, 0; -1, -1, +2, 0; and -1, -1, -1, +3) were significant for bodies, $F(1, 14) = 9.98, p = .007; 22.60, p < .001; and 24.62, p < .001$, respectively. Only the contrast (1, -1, -1, +3) was significant for trees, $F(1, 14) = 6.64, p = .022$. A similar pattern was observed for left EBA, such that all difference contrasts were significant for bodies: $F(1, 14) = 17.33, p = .001; 38.18, p < .001; and 20.48, p < .001$, respectively. For trees, only the contrasts (-1,
1, +2, 0) and (-1, -1, -1, +3) were both significant – $F(1, 14) = 8.45, p = .011$ and 9.30, $p = .009$ respectively, due to the fall in response to level 3 stimuli (branches).

In the right FBA, for bodies the contrast between levels 1 and 2 (-1, +1, 0, 0) was not significant, whilst the remaining comparisons (-1, -1, +2, 0; and –1, -1, -1, +3) were significant: $F(1, 14) = 11.71, p = .004$; and 42.47, $p < .001$, respectively. For trees, difference contrasts were non-significant for (-1, +1, 0, 0), but were significant for (-1,-1,+2, 0), $F(1, 14) = 9.93, p = .007$, and for (-1,-1,-1,+3), $F(1, 14) = 26.30, p < .001$. Note however that these significant effects are largely driven by the decrease in response at level 3 (branches) for the tree category. Polynomial contrasts revealed significant linear effects for bodies in all three ROIs, right EBA: $F(1, 14) = 28.42, p < .001$; left EBA: $F(1, 14) = 46.27, p < .001$ and FBA, $F(1, 14) = 42.38, p < .001$, but not for trees. Significant quadratic effects for bodies were found only in FBA, $F(1, 14) = 16.27, p = .003$.

**Discussion**

In sum, the EBA showed a linear increase in response to body parts as more of the body was made visible, whereas in the FBA the effect was more strongly second order; furthermore these effects were not present for the control stimuli. Although this pattern is consistent with a differential sensitivity to body parts and wholes, an alternative account of the EBA results must be considered. EBA lies in close spatial proximity to area hMT, which responds to implied visual motion in static displays of human figures (Kourtzi and Kanwisher, 2000). This raises the possibility that differences in the capacity for complex motion (i.e. whole bodies > arms > hands > fingers), and a significant contribution from area hMT, could explain the pattern we attribute here to the part-based analysis of bodies.
in EBA. In Experiment 3 we test this hypothesis by testing the response of hMT, and EBA to the stimuli used in Experiment 2. In Experiment 3, an event-related design was adopted to assess the suitability of the paradigm for a future ERP experiment.

**Experiment 3**

*Materials, methods and procedure*

Fourteen participants were tested. The stimuli were the same as those employed in Experiment 2. Each scan consisted of 340 2-second trials, comprising pseudo-randomized presentations of each of 16 images from eight stimulus categories, and a fixation condition. Each participant was tested on one of eight possible sequence orders. Each order was balanced so that every possible pair-wise sequence of conditions (including fixation) was presented equally often. Where the same condition occurred twice in succession, the identical stimulus item was presented 50% of the time. When this occurred, participants were required to press a response key. Image positions were jittered on alternate presentations to prevent participants from performing the 1-back task by detection of low-level transients. Within each trial, the image was displayed for 300 ms, followed by a 1700 ms fixation interval. In order to reduce fatigue, the sequence was scanned in two halves. Each half was padded with baseline fixation epochs of 16 seconds at the start and end of the run.

**Localisers.** In addition to the localiser scans used in Experiments 1 and 2, a third localiser was employed in order to identify motion-sensitive area hMT. Participants passively viewed alternating blocks of static and oscillating low contrast rings (c.f. Tootell, 1995). The experiment consisted of 21 15-second blocks. Blocks 1, 6, 11, 16 and
Body processing in EBA and FBA

21 were fixation only epochs. In the remaining blocks, static and moving stimuli were alternated.

All other scan parameters and data pre-processing procedures were identical to Experiment 2.

ROI analyses. ROI definition for EBA and FBA followed the procedure described in Experiment 1. Area hMT was defined by the contrast [moving rings] – [static rings]. For each participant individually, raw MR time-course values were extracted from the main experiment data, averaged across the voxels of each ROI. For each participant, raw average event-related timecourses were then computed, for each condition in each ROI, from 4 seconds pre-stimulus to 16 seconds post-stimulus. These timecourses were converted to percent signal change (PSC) values against the average evoked response to fixation, separately for each ROI in each participant, and separately at each TR in the evoked-response window. PSC was calculated as PSC = (MRc – MRf / MRf) x 100, where MRc is the average raw MR signal for an experimental condition and MRf is the average raw MR signal for the fixation condition. PSC timecourses were then averaged across participants and plotted to allow visualisation of the hemodynamic response. The time-point of the HRF (hemodynamic response function) peak (+4 seconds, relative to stimulus onset, see Figure 4) was identified from the group average graphs and individual PSC values at this time-point were then subjected to analysis by repeated measures ANOVA.

Results
Localisers. The EBA was identified, bilaterally, in all participants. Area hMT was localised bilaterally in 13 of 14 participants. Although the right FBA could be localised in nine participants ($p < .0001$) plus a further three at a more liberal threshold ($p < .005$), individual subject time-course data, collapsed across conditions, revealed weak or noisy stimulus dependent HRFs in seven of these cases. Thus, for reasons of poor signal:noise and a significantly reduced data set, further analysis of FBA was not attempted.

The mean spatial coordinates (with standard errors) of these regions, in Talairach space, were: left EBA: $X$: -44(1.2), $Y$: -72(1.4), $Z$: 4(1.5); right EBA: $X$: 47(1.1), $Y$: -69(1.4), $Z$: 5(1.4); FBA: $X$: 41(1.2), $Y$: -45(1.9), $Z$: -13(1.4); left hMT: $X$: -41(1.4), $Y$: -68(1.9), $Z$: 0(1.1) and right hMT: $X$: 46(1.6), $Y$: -65(1.4), $Z$: 3(1.1).

Analyses of EBA and hMT. Initial analyses were conducted on EBA and hMT to determine any influence of cerebral hemisphere. The EBA revealed a significant main effect of hemisphere, $F(1, 12) = 5.32, p = .04$ (left > right), but hemisphere did not interact with any other factors. No effects of hemisphere were found in hMT. On these grounds, further analyses were conducted combining data across hemispheres.

In a direct comparison of EBA and hMT (ROI x category x level), all main effects were significant: ROI $F(1, 12) = 8.37, p = .01$; category $F(1, 12) = 30.78, p < .001$; and level $F(3, 36) = 4.80, p = .006$. All two way interactions were significant: ROI x category $F(1, 12) = 17.49, p = .001$; ROI x level $F(3, 36) = 4.97, p = .005$; and category x level $F(3, 36) = 11.13, p < .001$. Critically, the three-way interaction (ROI x category x level) was also significant $F(3, 36) = 6.68, p = .001$. Plots depicting HRF timecourses for the
contrast [bodies – trees], at each hierarchical level and for each ROI, are presented in Figure 4.

Each ROI was then subjected to a 2 x 4 repeated measures ANOVA, testing the interaction of category and level. In the EBA, main effects of category and level were significant: $F(1, 12) = 32.167, p < .001$ and $F(3, 36) = 5.66, p = .003$, respectively, and the interaction of these factors was also significant, $F(3, 36) = 15.91, p < .001$. In hMT, the main effect of level was significant $F(3, 36) p = .04$, but the main effect of category and the interaction (category x level) were not significant.

A further analysis tested whether the interaction of category and level found in the EBA was stimulus-dependent -- that is, restricted to the peak of the HRF. The EBA data were analysed with a 2 x 4 ANOVA on difference scores (bodies-trees) at each level and at two time-points: stimulus onset (T = 0 sec) and HRF peak (T = 4 sec). Critically, the interaction of time x level was significant: $F(3, 36) = 4.95, p = .006$: differential effects of level were seen at the HRF peak, $F(3, 36)=15.91, p < .001$, but not at stimulus onset, $F(3, 36)=1.04, p = .39$. A similar analysis of hMT revealed no significant interaction of time x level, $p > .05$.

**Discussion**

These results demonstrate that the pattern of results attributed to the EBA in the previous two experiments is not due to the engagement of area hMT by images of body parts that may imply motion to varying degrees. The EBA discriminated between categories, and this effect depended on hierarchical level, as in the previous experiments.
Area hMT showed no such effects. Furthermore, analysis of selectivity time-courses (Figure 4) reveal no significant change in PSC magnitude between stimulus onset and peak in hMT, compared to a significant level x time interaction in EBA. Note that the functional discrimination of EBA and hMT was carried out using a conservative method: although the EBA and hMT peak voxels were separated in Talairach space, some spatial overlap was present between the ROIs (consistent with previous findings; Downing et al., 2001; 2007).

**General Discussion**

In this study we have differentiated the response properties of body selective regions in inferior temporal sulcus (EBA) and posterior fusiform gyrus (FBA). Our results show that a gradually increasing (and increasingly selective) response is elicited in the EBA to body parts in proportion to the amount of the body hierarchy that is visible. Furthermore, significant selectivity is seen even for the smallest hierarchical levels tested (e.g. single digits vs. single leaves). In contrast, the FBA shows a step-like rise in the response to torsos and headless bodies relative to images of smaller body parts. This region exhibited no significant selectivity for the two smallest levels of the hierarchy (fingers vs. leaves and hands vs. leaf clusters). These results provide the first evidence to date that the EBA and FBA make different contributions to the analysis of the appearance of the human body. In a third experiment we demonstrated that the findings in EBA could not be attributed to activity motion-selective area hMT; the dissociation of these two regions is noteworthy given their close proximity, and given previous findings of enhanced hMT responses to stimuli (such as bodies) that imply motion (Kourtzi and Kanwisher, 2000; Senior et al., 2000).
These findings are generally consistent with the proposed broad functional analogy between face and body sensitive areas of ventral occipitotemporal cortex. We suggest that the EBA’s representation of the body is relatively biased to the representation of individual parts. The FBA, in contrast, is not selective for small body parts and appears to preferentially represent larger portions of the body. Our findings of a strong response to the torso, and of relatively strong selectivity for arms (vs branches), however, indicate a representation that is not exclusively holistic (that is, tuned uniquely to the entire body form). Likewise, Schwarzlose et al. (2005) found significant responses to human body parts on the fusiform gyrus, with stimuli that depicted varying amounts of the body (R. Schwarzlose, personal communication, 20 Nov 2006). In this respect the FBA resembles FFA, in that that region also responds to some degree to face parts, e.g. to eyes (Tong et al., 2000), despite a preference for whole-body or whole-face stimuli, respectively. Further experiments, testing similar manipulations on bodies and faces simultaneously, will be needed in order to test how deeply the proposed analogy between face and body processing applies.

Part of the present model is supported by a recent study (Calvo-Merino et al., 2006) in which TMS was applied over the right EBA and to other sites. EBA stimulation disrupted a matching task on inverted but not upright body figures, whereas ventral premotor cortex (vPMc) stimulation had the opposite effect. The authors proposed that a parts-based analysis takes place in the EBA, which contributes to the task primarily when configural information – thought to be analysed in vPMc – is not available, due to the inversion of the stimuli.
If the EBA preferentially represents smaller parts of the body relative to the FBA, how might these areas interact in analysing the visual input? A strictly serial model, in which the EBA’s analysis of body parts is subsequently processed by the FBA, is probably too simplistic. Given the near ubiquity of bi-directional connectivity in visual cortex, it seems likely that if these regions indeed communicate, body representation would emerge from reciprocal signalling between the two areas. More evidence on the relationship between the EBA and FBA (and indeed vPMc) might be obtained with fMRI investigations of activation in these latter regions following deactivation of the EBA with transcranial magnetic stimulation (cf. Ruff et al., 2006).

We have interpreted our findings at the functional level to indicate that the EBA and FBA have different biases in the representation of body images. At the neural level these results are consistent with several scenarios. In the EBA, for example, the observed fMRI data could be due to a single unitary population of neurons with a complex tuning function that peaks for whole bodies and drops gradually for arms, hands and fingers. Previous findings from macaques (Desimone et al., 1984; Gross et al., 1972; Tanaka et al., 1991) and intracranial ERPs in humans (McCarthy et al., 1999) suggest instead the existence of individual neurons or groups of neurons highly tuned to visual features present in different body parts. Variants on this second model would account in different ways for the varying level of fMRI response as a function of the amount of the body that is visible. It may be the case, for example, that a larger proportion of neurons in the EBA is selective for visual features typically found in larger parts of the body, e.g. torsos, than for smaller parts, e.g. fingers. Alternatively, this region might contain roughly equal proportions of neurons tuned to features of different parts of the body. On this account,
the pattern of fMRI responses to fingers, hands, arms, and whole bodies can be explained by an asymmetry in the effect of these stimuli on the neural populations. For example, an image of an arm would (at least partially) engage neurons tuned to the visual features of fingers (as these would be present in their entirety within the image), and neurons tuned to features of hands, and of arms. In contrast, an image of a hand would engage only finger- and hand-sensitive neurons, leading to overall less neuronal activity and hence a weaker BOLD signal in the region.

In Experiments 1 and 2, we examined separately the left and right hemisphere EBA regions of interest. To date, the only systematic cross-hemisphere effects reported for the EBA involve viewpoint – right, but not left, hemisphere EBA shows a (slight but significant) preference for allocentric over egocentric views of bodies (Chan et al., 2004) and body parts (Saxe et al., 2005). Here we find some indication of subtle differences between the hemispheres, e.g. the significant interaction of left/right EBA with hierarchical level in Experiment 1, and the finding in Experiments 1 and 2 that the right EBA differs more robustly than the left EBA from FBA.

Our results may have some implications for future comparative fMRI studies. Pinsk et al. (2005; see also Tsao et al., 2003) scanned two macaques with fMRI while they viewed images of faces and body parts. Their results revealed distinct patches of body-part selective cortex in anterior and posterior regions of the superior temporal sulcus. The comparison of bodies and body parts applied in the present experiments may prove useful for understanding possible homologies between these regions and similarly selective regions in human cortex.
Finally, our findings raise questions about the neural and psychological representation of bodies and body parts in these and other brain regions. For example, psychologically, fingers, hands, and arms reflect natural subordinates of the general semantic category “human body”. Are the body representations in the EBA and FBA divided along these lines, or do they observe other principles that do not correspond to psychological boundaries? (Does the brain carve at the joints?) Similarly, we can ask whether different parts of the body are represented disproportionately, as found in the somatosensory and motor maps that surround the central sulcus. Further examination of these issues may indirectly provide insights into how the body representations in EBA and FBA relate to semantic, sensory, and motoric body representations elsewhere in the brain (see Schwoebel and Coslett, 2005, for a related discussion).

**Summary**

Our results shed light on two cortical representations of the appearance of the human body. They suggest an initial working hypothesis for the functional division of labour involved in the perception of other humans. They also point to future work using a variety of approaches to clarify how these regions carry out their computations, how they relate to other brain regions, and how they relate to cognitive, sensory, and motor knowledge of the body.
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29 Body processing in EBA and FBA


Figure Captions

**Figure 1.** Rendering of the cortical surface of one individual’s right hemisphere. Regions of interest are identified for illustrative purposes. Regions were defined by bodies or faces vs. tools, each at a threshold of $p < 0.0001$. EBA: extrastriate body area; OFA: occipital face area; FFA: fusiform face area; FBA: fusiform body area.

**Figure 2.** Results of Experiment 1. Mean response ($N = 10$) of left and right EBA and FBA, defined by [bodies + body parts] vs. [chairs + object parts], to fingers, hands, arms, and torsos. Error bars denote $SE$. Sample stimuli are given at the bottom of each chart.

**Figure 3.** Results of Experiment 2. Mean response ($N = 15$) to the four levels of each stimulus category in left and right hemisphere EBA and right FBA, as defined by the contrast [bodies + body parts] vs. [chairs + object parts]. Error bars indicate $SE$. Sample stimuli are given at the bottom of each chart.

**Figure 4.** Results of Experiment 3. Mean evoked response timecourses ($N = 14$) in EBA (left panel) and hMT (right panel) for the contrast “bodies – trees” at each of four hierarchical levels. Data reflect mean percent signal change from a fixation-only baseline condition. The zero point on the x-axis indicates time of stimulus onset. Sample stimuli are shown in the figure legend.
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Figure 4. Results of Experiment 3. Mean evoked response timecourses (N = 14) in EBA (left panel) and hMT (right panel) for the contrast bodies trees at each of four hierarchical levels. Data reflect mean percent signal change from a fixation-only baseline condition. The zero point on the x-axis indicates time of stimulus onset. Sample stimuli are shown in the figure legend.