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A Cortical Area Selective for Visual Processing of the Human Body

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Despite extensive evidence for regions of human visual cortex that respond selectively to faces, few studies have considered the cortical representation of the appearance of the rest of the human body. We present a series of functional magnetic resonance imaging (fMRI) studies revealing substantial evidence for a distinct cortical region in humans that responds selectively to images of the human body, as compared with a wide range of control stimuli. This region was found in the lateral occipitotemporal cortex in all subjects tested and apparently reflects a specialized neural system for the visual perception of the human body.

One of the most fundamental questions about visual object recognition in humans is whether all kinds of objects are processed by the same neural mechanisms, or whether instead some object classes are handled by distinct processing "modules." The strongest evidence to date for a modular recognition system comes from the case of faces [(1), but see (2)]. In contrast, relatively few studies have considered the mechanisms involved in perceiving the rest of the human body. Neuropsychological reports suggest that semantic knowledge of human body parts may be distinct from knowledge of other object categories (3). In addition, functional neuroimaging studies have implicated regions of the superior temporal sulcus (STS) in the perception of biological motion (4–6) and have associated regions of left parietal and prefrontal cortices with knowledge about body parts (7). Finally, single-unit recording studies in monkeys have identified neurons in the STS

that respond selectively to the appearance of the body, including the face (8–9). None of these findings, however, provides conclusive evidence for a region in human visual cortex selectively involved in processing the appearance of human bodies. Here, we report a

series of fMRI studies that provide the first evidence for such a region.

Subjects in these experiments were scanned while viewing images of objects from several different categories. In 19 out of 19 subjects scanned, we found a region in the right lateral occipitotemporal cortex (Fig. 1) that produced a significantly stronger response when subjects viewed still photographs of human bodies and body parts than when they viewed various inanimate objects and object parts (10). We have provisionally named this candidate body-selective region the "extrastriate body area" or EBA (11). After identifying the EBA in each subject with these "localizer" scans, we then ran a new set of experimental scans in the same session, in order to measure the response of the EBA to a large number of other stimulus categories (Figs. 2 and 3). This procedure enabled us to characterize the response profile of this region to a variety of different kinds of visual stimuli (12) in order to test a number of alternatives to our hypothesis that the EBA is selectively involved in visual processing of the human body.

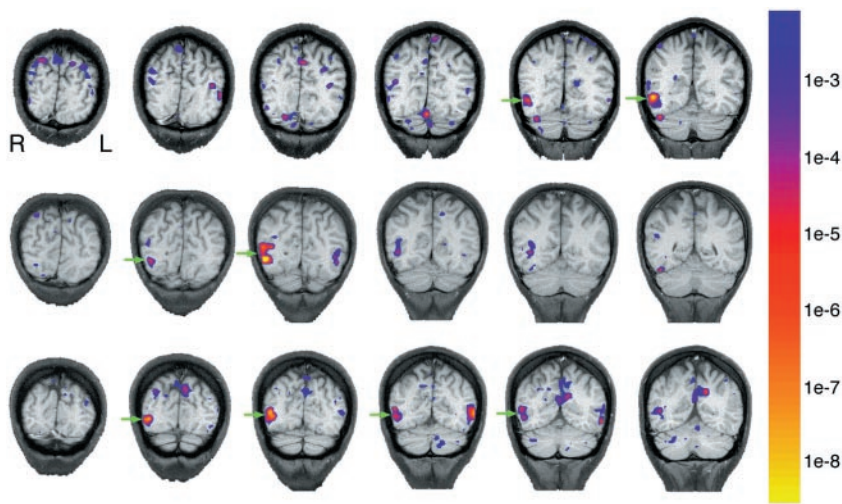


Fig. 1. EBA activations in three individual subjects. Each row shows coronal anatomical slices from a single subject, arranged from posterior (left) to anterior (right), overlaid with a statistical map showing voxels that were significantly more active for human bodies and body parts than for objects and object parts. The EBA is visible in the right occipitotemporal cortex of each subject (arrows); in some subjects an activation was also observed in the corresponding location of the left hemisphere. Scale indicates *P* value of activations in colored regions.

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In experiment 1, the response [percent increase in the MR signal (13) in the EBA] to human body parts (1.3%) and face parts (1.0%) was significantly greater than that to object parts (0.5%; $P < 0.001$ in each condition). It is noteworthy that the response to whole faces (0.6%) was significantly lower than to face parts ($P < 0.01$) and body parts ($P < 0.001$) and no greater than that to whole objects (0.5%; $P > 0.20$) (14). Experiment 2 revealed that the response to hands (1.4%) did not differ from that to assorted body parts (1.4%). In experiment 3, the response to human bodies (1.9%) was greater than that to human body parts [1.2%; $P < 0.025$ (15)], which in turn was greater than that to object parts [0.4%; $P < 0.005$ (16)]. Thus, relative to the control conditions, the EBA responded strongly and selectively to a variety of pictures of human bodies and body parts, with the single exception of faces.

In order to minimize differences between body and nonbody stimuli on low-level image properties such as texture, shading, and spatial frequency composition, we measured the response of the EBA to line drawings. In experiment 2, the EBA response to body parts was greater than to object parts, whether represented as line drawings ($P < 0.005$) or as photographs ($P < 0.001$). Similarly, in experiment 4 we found a significantly greater response to entire bodies (1.6%) than to cars (0.7%; $P < 0.01$), whether they were presented as line drawings or photographs (17). To further rule out low-level visual confounds, in experiment 6 we tested the EBA response to stick figure representations and silhouettes of human bodies, compared with scrambled versions of the same stimuli. The response to stick figures (1.7%) was significantly higher than that to the control items (1.0%; $P < 0.01$). Likewise, the response to human silhouettes (1.8%) was greater than that to scrambled versions (1.0%; $P < 0.05$). Finally, experiment 5 showed that the EBA does not respond generally to any object that, like the human body, is composed of rigid subparts connected at flexible joints. The EBA response to common articulated inanimate objects such as scissors (0.7%) was significantly lower than to bodies (1.5%; $P < 0.005$) and body parts (1.3%; $P < 0.005$) and did not differ from that to object parts (0.7%). We conclude that the selectivity of the EBA for body stimuli is not due to differences in the surface or structural properties of the stimuli (18).

Previous reports [e.g. (19)] have shown greater responses to animals than tools in a region near the EBA (in addition to an activation in the lateral fusiform gyrus), raising the question of whether the EBA is more generally responsive to all animals, rather than specifically to humans. In experiment 3, the response to nonhuman mammals (1.0%)

Fig. 2. Stimulus examples. The EBA response was high to human body parts (A) and whole human bodies (B) whether presented as photographs, line drawings (C), stick figures (D), or silhouettes (E), and was not attenuated to images that depict little implied motion (F). The low response to whole faces (G) was the single exception found to the preference for human bodies. In contrast, the EBA response was significantly lower to object parts (H) and whole articulated objects (I), whether represented as photographs or line drawings (J), as well as to scrambled control versions of stick figures (K) and silhouettes (L). The responses to face parts (M) and to mammals (N) were intermediate.

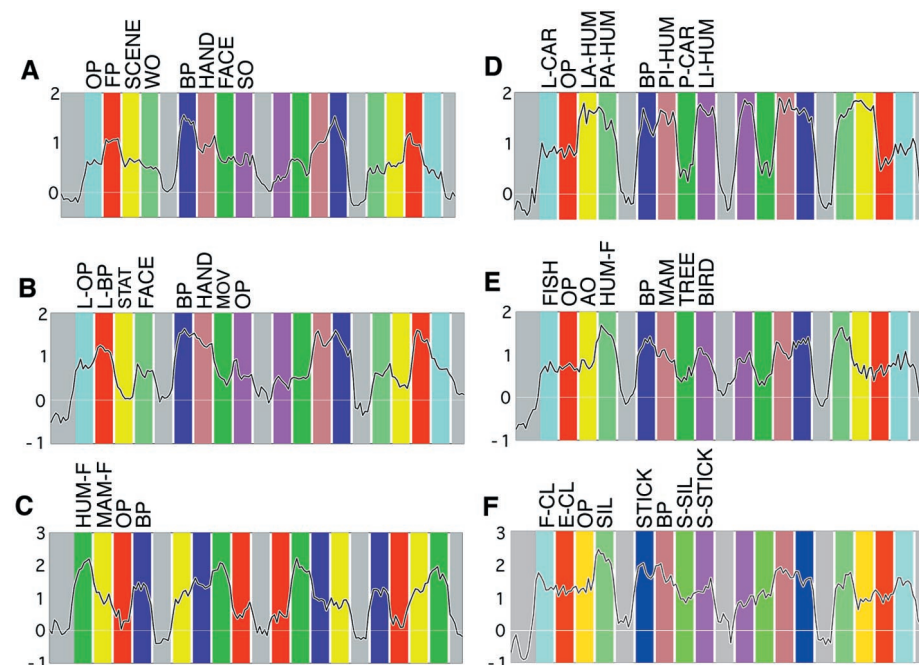


Fig. 3. Grand mean activation time courses from experiments 1 to 6 [(A) to (F), respectively]. Each block is indicated with a color band; repetitions of conditions within a scan are indicated by shared color. Data are in terms of percent signal change from fixation baseline (shown in gray). All data were extracted from regions of interest defined in independent scans, in each subject, within a session. Conditions in all experiments are labeled as follows (some conditions superseded by other analyses are not discussed here): OP, object parts; BP, human body parts; FACE, faces; HAND, hands. (A) FP, face parts; SCENE, outdoor scenes; WO, whole objects; SO, scrambled objects. (B) L-OP, line drawings of object parts; L-BP, line drawings of body parts; MOV, oscillating low-contrast rings; STAT, static low-contrast rings. (C) HUM-F, human bodies, without faces; MAM-F, mammal bodies, without faces. (D) P-CAR, photographs of cars; L-CAR, line drawings of cars; PA-HUM, photographs of alert humans; LA-HUM, line drawings of alert humans; PI-HUM, photo of inactive humans; LI-HUM, line drawings of inactive humans. (E) HUM-F, human bodies, without faces; MAM, mammals; BIRD, birds; FISH, fish; TREE, trees; AO, articulated objects. (F) F-CL, filled clothes; E-CL, empty clothes; SIL, human silhouettes; STICK, human stick figures; S-SIL, scrambled silhouettes; S-STICK, scrambled stick figures.

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was significantly lower than that to humans (1.9%; $P < 0.01$) and human body parts (1.2%; $P < 0.05$), but greater than that to object parts (0.4%; $P < 0.001$). In experiment 5, we tested several animal categories, revealing that the responses to nonhuman mammals (1.0%), birds (0.9%), and fish (0.8%) were all significantly below that to human bodies (1.5%; $P < 0.01$, $P < 0.005$, $P < 0.005$, respectively). Further, the response to mammals was only marginally higher than that to articulated objects (0.7%; $P < 0.08$), and this difference was not significant for birds or fish. Thus the EBA responds selectively to humans as opposed to other animals, with a possible modest preference for nonhuman mammals as opposed to other animal categories. However, this region is clearly not selective for the category of animals in general.

To further assess the relationship between the EBA and other visually selective cortical regions (Fig. 4), we tested for anatomical overlap (20) between the EBA and the following: retinotopic cortex (21), the fusiform face area (FFA) (22), the parahippocampal place area (PPA) (23), the lateral occipital complex (LOC) (24), and the visual motion area MT/V5 (25). We found no anatomical overlap between the EBA and retinotopic cortex, the FFA, or the PPA, as functionally defined in each subject individually. In some subjects, the EBA overlapped partially with either area MT or LOC (26). However, in 11

out of 11 subjects, a set of voxels was uniquely activated in the EBA localizer and not in either the MT or LOC localizers (mean 1.5 cm³, SEM 0.33 cm³). Thus, the EBA is clearly distinct from these other previously described visual regions (27).

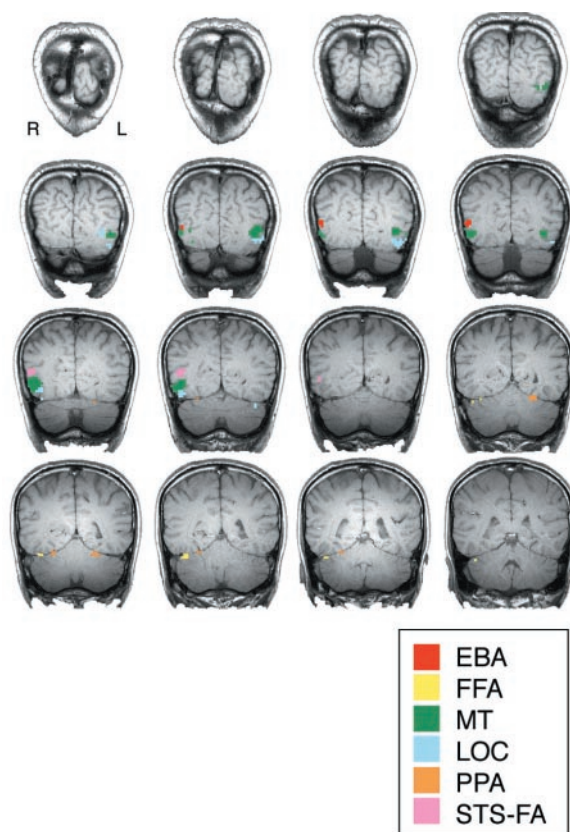
In conclusion, our results reveal a region in human lateral occipitotemporal cortex that responds selectively to visual images of human bodies and body parts, with the exception of faces. These findings suggest that the EBA is a specialized system for processing the visual appearance of the human body. At present, we can only speculate on the precise functional role of the EBA. It may be involved in the identification of individuals, perhaps under conditions in which face recognition is not possible (e.g., when the face is not visible because of viewing direction, distance, occlusion, poor lighting, and so on). Alternatively, the EBA may be critical for perceiving the position and/or configuration of another person's body, perhaps as part of a broader system for inferring the actions and intentions of others. Finally, it may be involved in perceiving the configuration of one's own body, for example in the guidance of actions.

In its strong selectivity for a specific object category, the EBA resembles other previously identified regions of human extrastriate cortex such as the FFA and the PPA. Although all three respond somewhat to non-

preferred stimuli, each shows a general and strongly selective response to stimuli from its preferred category. The existence of these category-selective regions in human extrastriate cortex supports the hypothesis that high-level vision is not accomplished by a single functionally undifferentiated system. Rather, visual perception and cognition appear to be served by distinct mechanisms for at least a select few categories, including faces, places, and bodies.

How many category-specific regions like the EBA exist in human extrastriate cortex? In ongoing studies, we have tested a wide range of other object categories and have so far found no compelling evidence for other category-selective regions in occipitotemporal cortex. This result suggests that objects from many categories may be represented by a "general-purpose" recognition system, a role proposed for the lateral occipital complex (28, 29). Perhaps the most fundamental unanswered question about category-selective regions in human extrastriate cortex concerns the origins of these structures. Are the FFA, PPA, and EBA largely specified in the genome, or do these regions primarily derive from the extensive lifetime experience an individual has with faces, places, and bodies? Methodological advances now being developed may enable us to answer even these most challenging questions about the organization and origins of object representations in the human brain.

Fig. 4. Coronal slices from a single subject, arranged from posterior (top left) to anterior (bottom right), showing the EBA, FFA, MT, LOC, PPA, and face-selective region of STS, all identified within a single scanning session. Colored voxels are those which reached significance ($P < 10^{-7}$) in a standard localizer scan for each region; regions of overlap are not indicated.



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10. Scanning was conducted on a 1.5 T (experiments 1 to 6) or 3.0 T (experiment 7) Siemens scanner at the Massachusetts General Hospital-NMR center in Charlestown, MA. The general procedure was identical in all experiments. A gradient echo pulse sequence (TR = 2 s) was used. Sixteen to 20 slices (4 to 6 mm thick, 3.125 mm by 3.125 mm in-plane resolution) were collected using a standard head coil. The slices were either parallel to the brainstem, starting near the occipital pole and extending anteriorly to cover most of the occipital and parietal lobes and at least the posterior half of the temporal lobe, or axial, covering most of the cortex. Six subjects participated in experiment 1 and experiment 2 in the same session; of these, four also participated in experiment 3 in the same session. Five new subjects participated in experiments 4 and 5 in the same session. Six new subjects participated in experiment 6 (one of whom had participated in earlier studies), and three new subjects participated in experiment 7. In each experiment, photographs of human body parts and of object parts were included in separate blocks as baselines and as localizers for other scans. The remaining conditions in each experiment were as fol-

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- lows. Experiment 1: faces, face parts, hands (in a single configuration), whole objects, scrambled objects, and scenes; experiment 2: faces, hands (in multiple configurations), oscillating low-contrast rings, static low-contrast rings, line drawings of body parts, and line drawings of object parts; experiment 3: human bodies and mammals, both with heads removed, in separate blocks; experiment 4: photographs and line drawings of humans, both alert and inactive, and line drawings and photographs of cars; experiment 5: humans with heads removed, mammals, birds, fish, trees, and articulated objects; experiment 6: human silhouettes and scrambled versions, human stick figures and scrambled versions, empty and filled clothes; experiment 7: humans, mammals, chairs, tools, faces, and scenes. The stimuli in all experiments were gray-scale photographs (or line drawings where applicable) on a uniform background. In each experiment, 15 exemplars from each category were tested. Each scan consisted of 16 experimental blocks (16 s each) with a 16-s fixation-only period intervening every four blocks and at the beginning and end of the scan. Twenty images were presented individually within each block, each appearing for 300 ms followed by a fixation-only interval of 500 ms. Block order was counterbalanced between two versions of each experiment so that mean serial position in the scan was equivalent across conditions. Subjects were typically scanned four times on each experiment; scans from different experiments were interleaved in the same session. Subjects performed a 1-back repetition detection task during the scans, pressing a button whenever the same stimulus appeared twice in immediate succession, which occurred twice per block.
11. Regions of interest (ROIs) were defined as contiguous voxels in the occipitotemporal area of the right hemisphere where the response to human bodies/body parts was significantly greater than to controls at $P < 10^{-4}$ (uncorrected) on a Kolmogorov-Smirnov test. Many subjects also showed a substantially weaker but significant activation in the left hemisphere. The response properties of this left hemisphere ROI were measured where possible and found to closely match the right hemisphere; only the right hemisphere data are reported here. For analyses concerning overlap with other cortical areas (described below), both hemispheres were considered. We also determined the average (with standard deviation) across seven subjects of the MNI coordinates of the most significant voxel in the EBA: [51 (2), -71 (4), 1 (3)] for the right hemisphere and [-51 (4), -72 (5), 8 (4)] for the left hemisphere. [We report MNI coordinates (based on the Montreal Neurological Institute (MNI) probabilistic brain atlas) as they are based on the average of many brains rather than a single one, and they are the native coordinate system of the widely used SPM package.]
 12. We focus here on the visual properties of this extrastriate region. These results do not exclude the possibility that stimulation in other modalities could activate the EBA (30). Other questions for future research include the possible role of the EBA in representing general, amodal semantic knowledge about the body, and the relation between the EBA and parietal and frontal systems involved in the representation and generation of actions (31).
 13. Mean time courses were extracted for each subject in each experiment, averaging across scans and across the voxels in the ROI. Percent signal change was determined for each subject and each condition relative to the fixation-only baseline epochs. Hemodynamic lag and mixing of effects at epoch boundaries were accounted for by assigning the first time point of each epoch to the previous condition, and dropping the subsequent time point. All reported data reflect grand mean percent signal change from fixation across subjects. The data used to calculate the percent signal changes in each condition were collected from different scans than those used to identify the ROIs.
 14. The low response to faces distinguishes the EBA from other apparently face-selective regions of the STS (32).
 15. It is not clear whether the higher response to whole bodies reflects a preference for whole bodies over body parts, or the presence in the stimulus of multiple undetached body parts. Both possibilities, however, are consistent with a representation in the EBA of the appearance of the human body.
 16. In experiment 3, we tested human bodies with heads removed to account for the possibility, suggested by the low response to faces alone, that faces might inhibit activation of the EBA. Whereas in experiment 3 the response to (headless) bodies was greater than to body parts, in experiment 4, the response to bodies with intact faces (1.5%) did not differ from that to body parts (1.5%), consistent with this inhibition hypothesis.
 17. Although a significant interaction between object type (body versus nonbody) and format (photograph versus line drawing) was found in experiment 2 ($P < 0.05$), this interaction did not reach significance in experiment 4 ($P > 0.1$).
 18. As bodies (unlike many man-made objects) have the capacity to move on their own, we also tested whether the implication of motion is necessary to produce the high EBA response to bodies observed here. In experiment 4, we compared photographs and line drawings of alert, upright humans with control pictures of the same individuals lying down with their eyes closed, as if asleep (33). No significant difference was found in the EBA response to alert (1.6%) compared with inactive (1.6%) people. Thus the implication of motion is not necessary to produce a strong response in the EBA.
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 20. The FFA was identified with a contrast comparing faces with objects; the PPA by comparing scenes with faces and objects; LOC by comparing intact with scrambled objects; and MT/V5 by comparing moving with static low-contrast rings. The FFA and PPA were localized with the relevant contrasts from experiment 1. The LOC, MT, and retinotopic areas were localized in separate scans concurrent with experiments 4, 5, and 7. Five additional subjects were scanned on LOC, MT, and EBA localizers to contribute to this analysis.
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 26. On average, 31% of EBA voxels (median 21%) were also significantly activated in either the MT or LOC localizers; in no subject was the overlap complete. There are several reasons why objectively discrete neural systems might appear to overlap as measured with fMRI. First, functionally independent neural networks might occupy the same region of cortex in an interdigitated fashion. Second, the boundary between two networks that are spatially discrete but adjacent is unlikely to fall exactly along voxel borders. Third, limits to the spatial resolution of the BOLD signal reduce the independence of the signal from adjacent voxels. As a result, fMRI methods cannot support definitive claims about the absence of overlap between adjacent neural systems. Thus the possibility of partial overlap between the EBA and MT/LOC cannot be decisively ruled out. However, the present evidence demonstrates that the EBA cannot be a complete subset of the other visual regions tested.
 27. We also considered the response of the EBA to biological motion displays (34). The independently localized EBA responded significantly more to point-light animations of biological motion than to scrambled controls ($P < 0.025$; $n = 10$). This result is consistent with our other findings, as the experimental stimulus suggests the presence of a human figure, whereas the control does not. We further tested the response of the EBA ($n = 5$) to gray-scale images of human bodies and articulated objects presented in short animation sequences. The motion sequences were either "artificial," in which the entire object appeared to oscillate rigidly around its midpoint, or "natural," in which the object moved in a realistic manner (e.g., a kicking motion in the human-object condition, or scissors opening and closing in the articulated-object condition). The EBA response was greater to natural motion than to artificial motion for both human bodies (2.2% versus 2.0%; $P < 0.025$) and for objects (1.2% versus 0.8%; $P < 0.01$). There were significant main effects of both motion type ($P < 0.005$) and object type ($P < 0.001$), but critically these two factors did not reliably interact. If anything, the increase in response to natural motion over artificial motion was greater for objects (0.4%) than for humans (0.3%). Further, the higher response for natural motion compared with artificial motion was also observed in area MT (in voxels that did not overlap with the EBA); for bodies (2.7% versus 2.3%; $P < 0.05$) and objects (2.4% versus 1.8%; $P < 0.001$), and this effect did not significantly differ from the same effect seen in the EBA. These findings in both the EBA and MT do not depend on using artificial motion as the control; the same pattern of data and statistical significance held when natural motion was compared with static images. This suggests a generalized (perhaps attentional) enhancement of the response to the natural-motion stimuli, whether bodies or objects. Thus, although the EBA is sensitive to motion information, it has no specific preference for biological motion per se.
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