



The effect of viewpoint on body representation in the extrastriate body area

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Functional neuroimaging has revealed several brain regions that are selective for the visual appearance of others, in particular the face. More recent evidence points to a lateral temporal region that responds to the visual appearance of the human body (extrastriate body area or EBA). We tested whether this region distinguishes between egocentric and allocentric views of the self and other people. EBA activity increased significantly for allocentric relative to

egocentric views in the right hemisphere, but was not influenced by identity. Whole-brain analyses revealed several regions that were influenced by viewpoint or identity. Modulation of EBA activity by viewpoint was modest relative to modulation by stimulus class. We propose that the EBA plays a relatively early role in social vision. *NeuroReport* 15:000–000 © 2004 Lippincott Williams & Wilkins.

Key words: EBA; Extrastriate body area; fMRI; Identity; Self; Viewpoint

INTRODUCTION

Human beings are a social species; as a result we pay a great deal of attention to the behaviour of others around us. Much research in cognitive neuroscience has been devoted to understanding the social vision systems of the brain: those processes that interpret the appearance and actions of other people in order to extract their social implications. Particular attention has been focused on visual perception of faces. Studies in humans and animals have identified a handful of cortical regions that are activated by face stimuli. Face-selective neurons are found in the macaque temporal lobe, particularly in the superior temporal sulcus [1,2]. In humans, a region of posterior fusiform gyrus (fusiform face area, FFA) responds generally and selectively to human faces in fMRI studies [3,4]. A nearby ventral occipital region (occipital face area, OFA) shows similar selectivity but has not been as well studied [5]. Direct cranial recordings reveal face-selective electrophysiological responses in the ventral temporal region [6], and scalp ERPs reveal face-selective negativities at lateral posterior sites [7,8]. Face selective fMRI responses are also seen in the posterior superior temporal sulcus (STS), particularly to animations of facial expressions or mouth movements [9,10].

The rest of the body, aside from the face, also provides substantial information about other individuals, including identity, gender, and emotion. The posture and movement of the body provide clues about others' intentions through their actions. A number of findings from single-unit neurophysiology implicate macaque STS in the representation of posture, action, and intention [11,12]. For example, many neurons in anterior STS respond selectively to views of humans or monkeys performing particular actions or holding specific poses [13]. FMRI in humans has shown that regions of STS activate to both point-light and naturalistic displays of biological motion [14–17].

A recent fMRI study identified a region of human cortex that responds generally and selectively to images of the human body [18]. This extrastriate body area (EBA), is found bilaterally at the posterior end of the inferior temporal sulcus. A series of studies showed that this region responds strongly to images of humans (both moving and static) presented in a variety of formats (e.g. photographs, line drawings, silhouettes), relative to perceptually-matched control objects.

This selectivity for the human figure suggests that the EBA could be involved in the extraction of visual information about other individuals. To date, however, the functional role of the EBA remains unclear. Its response to bodies could reflect an identification system that distinguishes among other individuals. In contrast, it may be involved in interpreting the actions of other people. These possibilities focus on the perception of others, but the EBA could also play a role in perception of the self, for example by providing a visual representation of the position of one's own limbs. A recent report goes further to suggest that the EBA is involved in the generation of limb movements, even when those movements are not visible [19]. This latter finding has the possible implication that the EBA provides information for other cortical regions (e.g. in STS) about whether body stimuli in the visual image belong to the self or to another individual [20].

Here we used fMRI to test whether the EBA responds more to egocentric than to allocentric views of bodies. By egocentric views, we mean those that one would typically have of one's own body, and by allocentric views, we mean those that one would typically have of others' bodies. This variable is crossed orthogonally with a manipulation of whether the body viewed is the self or another familiar person. If the EBA primarily supports the visual representation of one's own body, then it should respond more to

egocentric views, particularly of the self. In contrast, if the EBA is primarily involved in perceiving others, then allocentric views, especially of other people, should produce greater activation. Finally, if the EBA is involved at more primitive levels of processing body-related information, then these manipulations would be expected to modulate EBA activity relatively weakly.

MATERIALS AND METHODS

Participants: Ten healthy adult volunteers (five female) were recruited from the University of Wales, Bangor community. Participants satisfied all requirements in volunteer screening and gave informed consent. Ethics approval was obtained from the School of Psychology at the University of Wales, Bangor and the North-West Wales Health Trust. Participation was compensated at £20 per session.

Stimuli: Before scanning, each volunteer was photographed in colour, while holding 20 different poses. A variety of seated and standing poses were photographed, some of which included most of the body, while others included primarily the upper torso or the lower half of the body. All images excluded volunteers' heads. In order to match body configurations as closely as possible across conditions, each pose was photographed twice: once from an allocentric perspective, and once from an egocentric perspective (see Fig. 1 for examples). Allocentric views were taken from a distance of about 1 m from the volunteer. Egocentric views were shot by placing the camera directly in front of the volunteer's eyes. The same poses were used across participants.

Scanning protocol: A 1.5T Philips MRI scanner with a parallel head coil was used. For functional imaging, an EPI sequence was used (TR=3000 ms, TE=50 ms, flip angle=90°, FOV=240, 30 axial slices, 64 × 64 inplane matrix, 5 mm slice thickness). The scanned area covered the whole cortex and most of the cerebellum. Functional data were manually co-registered with 3D anatomical T1 scans (1 × 1 × 1.30 mm resolution).

Design and procedure: There were 21 15s blocks per scan. Blocks 1, 6, 11, 16, and 21 were a fixation-only baseline condition. In the four intervening sets of four blocks, each of the four conditions (self/other × egocentric/allocentric) occurred once, in a different order for each set. Each condition appeared once at each serial position across the four sets. Two versions of the block order were constructed. The first half and second half of one version were swapped to create the second version. The order of blocks was symmetrically counterbalanced within each version, so that the first half of each version was the mirror order of the second half. The result is that the mean serial position of each condition was equated. Within each block, 20 exemplars from one condition were presented. Each stimulus appeared for 300 ms, followed by a blank inter-stimulus interval of 450 ms.

Participants were scanned in two groups of five. Within each group, all volunteers were very familiar with the others (e.g. were members of the same lab or shared office space). Within a group, images of the same five people were

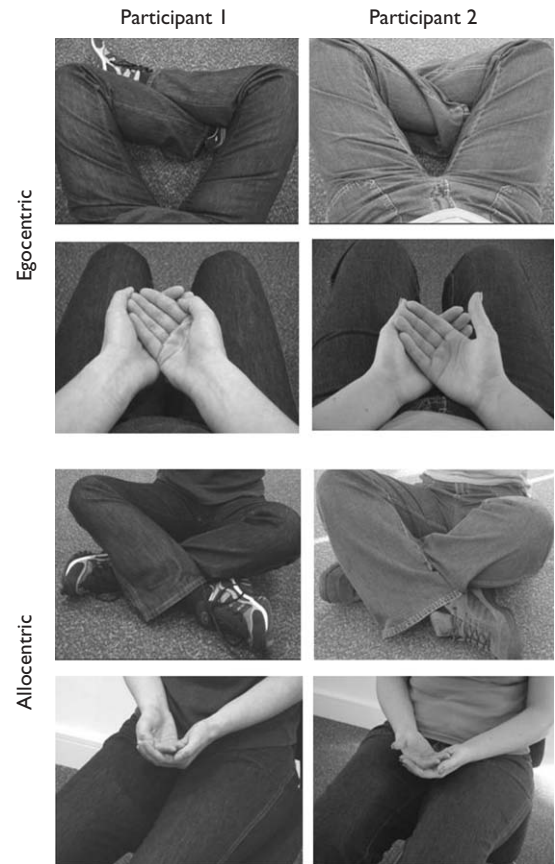


Fig. 1. Sample stimuli from the experiment. Each column shows images from a different participant. The first two rows give examples from the egocentric viewpoint, and the last two rows give examples from the allocentric viewpoint.

presented, with the assignment to self or other condition depending on the identity of the participant. The stimuli for a given block in the other conditions were images of a single individual. Each of the four other individuals appeared equally often in each scan. Before the session began, participants were informed of the identities of the people they would be viewing.

All participants were also scanned on four runs of a localiser experiment to identify the location of the EBA. Forty full-colour images of faces, bodies, scenes, and tools were presented, with each category in a separate block. The design and procedure of this study were similar to that of the primary experiment.

In all scans, participants performed a 1-back repetition-detection task. They were asked to press a button whenever an image occurred twice in immediate succession. Two image repetitions occurred at randomly-selected points in each block.

Visual stimuli were projected onto a back-projection screen located behind the participants' head. Participants viewed images in a tilted mirror attached to the head coil.

Image analysis: Imaging data were analysed using Brain-Voyager software Version 4.9 (BrainInnovation, Maastricht, The Netherlands). The first two functional images of each scan were dropped from the analysis to avoid differences in

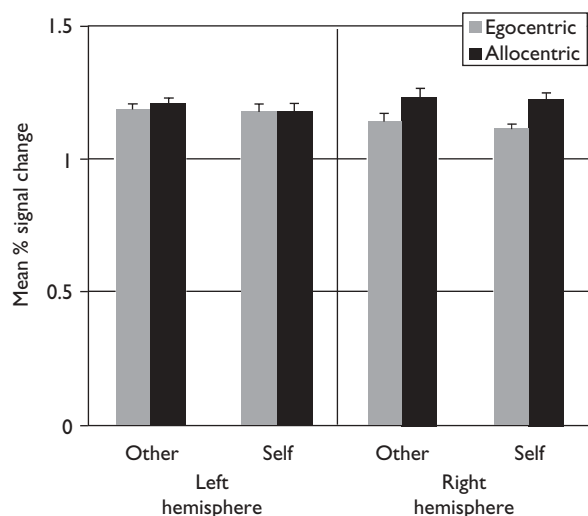


Fig. 2. Average percentage signal changes (PSCs) from the independently-localised EBA. Error bars reflect within-subjects s.e.m.

T1 saturation. Pre-processing of functional images included: 3D motion correction of functional data using trilinear interpolation, temporal high pass filtering (0.006 Hz cutoff), and spatial smoothing with a Gaussian kernel (full width, half maximum 6 mm). The 3D scans were transformed into Talairach space, and the parameters for this transformation were applied to the co-registered functional data.

In order to generate predictors for multiple-regression analyses, the event time series for each condition were convolved with a model of the hemodynamic response. Voxel time series were z-normalized for each run, and additional predictors accounting for baseline differences between runs were included. For the primary analysis, the left and right EBA regions of interest (ROIs) were defined for each subject by contrasting bodies *vs* the average of faces, tools, and scenes, at a threshold of $T > 9.0$. Whole-brain group-average analyses were also tested in a random effects model at a significance threshold of $p < 0.001$ (uncorrected) and an extent threshold of 100 mm^3 .

RESULTS

Behavioural results: The mean (\pm s.e.) d' for 1-back target detection was 3.4 ± 0.14 ; this value did not vary significantly by condition ($F < 1$, ns). After the scanning session, all participants reported that they were easily able to identify the individuals they had seen in the study.

fMRI results: All subjects showed a significant EBA activation in both hemispheres (mean Talairach co-ordinates: right, 46, -69, 1; left, -45, -73, 4) in the localiser scans. Activation values from these ROIs were extracted for each condition (Fig. 2). These values were the mean percentage signal change for each condition, relative to the mean signal in the fixation-only baseline epochs. Percentage signal changes were extracted for each scan separately and then averaged for each subject, resulting in one value per condition per subject. An ANOVA on these data, with view, identity and hemisphere as within-subjects factors, resulted in a significant three-way interaction ($F(1,9)=8.3$, $p < 0.05$), an interaction of view \times hemisphere ($F(1,9)=33.1$, $p < 0.001$), and a main effect of view ($F(1,9)=10.0$, $p < 0.05$).

Table 1. Results of whole-brain, random-effects analyses.

Area	Talairach coordinates			mm ³	Mean T
	X	Y	Z		
Egocentric > Allocentric					
L. Superior parietal	-40	-48	52	2036	6.16
Allocentric > Egocentric					
R. Lateral occipital	27	-88	-2	1326	5.43
R. Parahippocampal gyrus	19	-41	-8	554	5.28
R. Cuneus	17	-61	17	2085	5.99
L. Parahippocampal gyrus	-17	-47	-2	2741	6.07
Other > Self					
R. Anterior STS	56	-14	-8	549	5.22
R. Cerebellum	25	-32	-23	243	5.29
R. Striatum	18	-11	-7	708	5.43
R. Medial anterior occipital	5	-51	9	626	5.68
L. Cuneus/precuneus	-3	-61	29	3779	5.85
L. Anterior STS	-59	-8	-2	235	5.10

To follow up the three-way interaction, additional tests were conducted within each hemisphere separately. In the right hemisphere, there was a significant main effect of view ($F(1,9)=28.1$, $p < 0.001$), with a larger response to allocentric relative to egocentric views. Neither the main effect of identity, nor the interaction of identity and view were significant (both $p > 0.4$). The left EBA showed no significant effects (all $p > 0.35$).

The whole-brain analysis revealed significant main effects of viewpoint and of identity in several regions (Table 1). No regions showed a significant interaction between the two variables.

DISCUSSION

We find that the right hemisphere EBA responds more to allocentric views of people than to egocentric views, while the left EBA does not discriminate between these conditions. The preference in the right hemisphere for allocentric views may suggest an early stage in the social vision system. That is, the bias for others seen in the right EBA could be further amplified and refined in right superior temporal sulcus regions responsible for perceiving other people [10]. The significant interaction with hemisphere also suggests that the view effect found in the right EBA is not due to a stimulus confound or to general factors such as attention or arousal, which would be expected to operate equally in both hemispheres.

We speculate that this hemispheric asymmetry reflects a general bias toward more abstract object representations in the left hemisphere relative to the right hemisphere. For example, recent behavioural and fMRI studies suggest that object-selective cortical regions are view-independent in the left hemisphere and view-dependent in the right hemisphere [21,22]. In neither hemisphere does the EBA distinguish between views of the self and views of highly familiar others. This suggests that the image properties selected by the EBA are not of sufficient detail to distinguish between different individuals.

In absolute terms, the modulation of the EBA response by identity and viewpoint was relatively small, and all of the conditions evoked a strong absolute response. This is in contrast to the modulation of EBA activity by stimulus class.

The ratio of response to bodies relative to other kinds of inanimate objects typically approaches 2:1 [18]. Taken together, these findings imply that the EBA is primarily selective for image features that distinguish between human bodies and other kinds of objects. Previous work [18] has shown that these features must be relatively high-level, given that selectivity for human forms is preserved when they are represented as line drawings, stick figures, or silhouettes.

Future research may yet reveal a stronger influence of identity and viewpoint on EBA activity. In the present study, while differences in identity and viewpoint were readily apparent to subjects, these variables were not relevant to the one-back memory task. It may be that sensitivity to higher-level dimensions in the EBA only emerges when they are relevant to current processing demands. Additionally, the use of closed-loop stimuli, in which participants view live video of either their own actions or those of others, may create a stronger impression of ownership of the images related to one's own body parts. For example, in a recent study subjects viewed either normal or left/right inverted live video displays of their own manual actions [23]. The inverted display produced more activity than the normal condition in a region near the EBA, which could reflect a role for the EBA in the coupling of proprioception and visual information about one's own limbs. However, this study did not include conditions in which the actions of others were viewed.

Several activations from the whole brain analysis were noteworthy. First, a region of the left superior parietal lobe was more active to egocentric than allocentric views, consistent with a role for this region in representing nearby stimuli in body-centred coordinates [24]. Second, allocentric views produced bilateral activation in the posterior parahippocampal gyrus, a region that represents views of the local environment [25]. We speculate that this was due to the presence in some allocentric images of parts of the background. Finally, viewing others, relative to the self, produced activity in the anterior STS bilaterally, suggesting that the absence of a self/other distinction in the EBA was not due to an ineffectual manipulation. This result is consistent with a role for the STS in the perception of the behaviour of others [10].

CONCLUSION

While the EBA does not distinguish the self from familiar others, it does (in the right hemisphere) distinguish allocentric from egocentric views of bodies. This finding suggests that the EBA plays an early role in parsing body-related visual stimulation, by distinguishing that which is associated with the viewer's body schema from that which is not [20].

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