Your hand or mine? The Extrastriate Body Area

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ABSTRACT

Visual images of our own and others' body parts can be highly similar, but the types of information we wish to extract from them are highly distinct. From our own body we wish to combine visual information with, at least, somatosensory, proprioceptive and motor information in order to guide our interpretation of sensory events and our actions upon the world. For others' bodies we only have visual information available, but from that we can derive much useful social information including their age, health, gender, emotional state and intentions. Consequently, a challenge for the brain is to sort visual images of our own bodies, to be integrated with processing from other sensory modalities, from highly similar images of others' bodies for social cognition. We explored the possibility that the Extrastriate Body Area (EBA) may help to accomplish this sorting. Previous work had suggested that the EBA is responsive to images of both our own and others' body parts but does not distinguish between them. Here, using fMRI adaptation, we provide evidence that the right EBA contains separate neural sub-populations that are selectively sensitive to images of our own or others' body parts. Thus, we argue that the right EBA may perform an important sorting of body part images by identity (including self-recognition) and may interact both with brain areas involved in sensory processing and social cognition having identified our own and others' body part images respectively.

INTRODUCTION

The EBA is a region of the lateral occipitotemporal cortex that has been shown, using neuroimaging, to be selective for images of the human body (Downing et al., 2001). Converging evidence for the selectivity of this region comes from the observation that transcranial magnetic stimulation to the EBA impairs performance on a body part matching task but not face part matching (Urgesi et al., 2004). To date the involvement of the EBA in a small number of functions including the perception of moving bodies (Downing et al., 2006) and biological motion (Peelen et al., 2006; Grossman and Blake, 2002), the performance of motor actions (Astafiev et al., 2004; Peelen and Downing, 2005; Astafiev et al., 2005) and viewpoint dependent processing of body parts (Chan et al., 2004; Saxe et al., 2005) has been explored (for a review see Peelen and Downing, 2007).

It has been further speculated that an important role of the EBA may be its involvement in the perception of one's own vs. another's body (Downing et al., 2001, but see Peelen and Downing, 2007; Jeannerod, 2004). Comparable differential processing has already been demonstrated with human faces. For instance, PET measurements indicate selective activation of brain regions including the fusiform gyrus, the locus of the proposed 'fusiform face area' (FFA) (Kanwisher et al., 1997), to blocks of stimuli containing one's own face compared to those containing only others' faces (Sugiura, et al., 2000). Furthermore, differential processing within the FFA related to one's own vs. others' racial group membership has also been reported (Phelps, 2001). An initial investigation of the EBA capacity to distinguish own from other body images was conducted by Chan, Peelen and Downing (2004). They reported that the EBA showed no difference in activation to images of one's own

body compared to images of others' bodies. They interpreted their finding as evidence that the EBA does not distinguish between individuals and does not therefore have an ability to recognize oneself. However, the method used in their study leaves open the contrary possibility. This is because fMRI has a relatively coarse spatial resolution, reflecting the average activity of neural populations contained in several cubic millimeters of the brain's volume. Consequently, a standard fMRI analysis that contrasts activity between two different experimental conditions, in a previously localised region of interest, to explore the relative selectivity of neural populations in that region will not be able to distinguish the functional role of separate but interleaved neural populations within voxels (three dimensional volumes in the brain) in that region. It is entirely possible that within EBA voxels there are separate neural networks that are selectively activated by either own or other body images. In a standard contrast analysis, because both types of image could result in equal activation of different neural networks within the same voxel(s), no difference would be observed.

Consequently, here we exploit the fMR-Adaptation (fMR-A) technique (Grill-Spector et al., 1999; Grill-Spector and Malach, 2001), to overcome this limitation of standard contrast methods and determine whether the EBA contains networks that distinguish our own from others' body parts. fMR-A has already been successfully used in the EBA to demonstrate the action selectivity of neural sub-populations in this region (Kable and Chatterjee, 2006). The basic premise of fMR-A is that repeated presentation of the same image, or different images that a functional area does not distinguish, will result in a decreasing haemodynamic response to the stimuli (Henson et al., 2000; Grill-Spector et al., 2006) known as repetition suppression or adaptation.

Conversely, presentation of a stimulus that is processed by a different neural network in the same cortical area will result in a rebound from adaptation. Thus, the extent of adaptation provides an index of to what extent a given cortical area contains neural networks that are selective for particular types of difference between stimuli.

In a first experiment, using the fMR-A approach, we characterized the effect of neuronal adaptation in the EBA. Participants viewed body part images in blocks with 1, 2, 4, 8 or 32 different images in a block. We expected that, if the EBA distinguishes between body part images, then activity would reduce, due to adaptation, as the number of different body part images presented in a block decreases. In a second experiment, we explored the capacity of the EBA to represent different individuals' body parts by comparing adaptation to blocks of 1, 2 or 6 different hand images. If the EBA distinguishes between individuals then we should expect that activity will reduce, due to adaptation, as the number of different hand images presented in a block decreases. Finally, we examined whether the EBA separately represents one's own body parts by comparing adaptation in blocks with images of two other individuals' hands to adaptation in blocks with images of one's own and another's hand. If the EBA has separate networks to sort images of one's own body parts from those of others then we should expect less adaptation in the block that includes images of one's own hand.

METHOD

Participants

Twelve participants were recruited for the first experiment (4 male) and 15 for the second experiment (6 male). All participants had normal or corrected-to-normal vision. Scanning took place on the Siemens Trio 3T scanner at the CUBIC imaging facility, Royal Holloway, University of London, UK. Participants were screened in accordance with the imaging facility's standard protocols and written consent was also obtained prior to scanning. Ethical approval was granted by the University of Surrey Ethics Committee.

Task and Procedures

The EBA localizer

In both experiments two EBA localizer runs were used to identify the EBA for each participant, a sample EBA run is shown in figure 1. The stimuli were similar to those used previously to localize the EBA (Downing et al., 2001) and were grayscale photographs ($12.33^\circ \times 15.81^\circ$ visual angle).

INSERT FIGURE 1 HERE

Each run lasted 340s (136 volumes; TR = 2500ms; 42 axial slices; 3mm slice thickness; 64x64 inplane resolution; 3x3x3mm matrix) and comprised four blocks of grayscale body part stimuli, four blocks of grayscale object stimuli and five fixation blocks. Each experimental block lasted 30s (12 volumes) and contained 45 exemplars

of the category. Within blocks each stimulus was presented for 542ms, with an ISI of 125ms. Fixation blocks consisted of a fixation cross ($1.42^\circ \times 1.42^\circ$ visual angle) with a duration of 20s (8 volumes). Both runs were counterbalanced by reversing the block orders within the run and participants were instructed to covertly name each stimulus in order to maintain attention during the task.

Experiment 1: discrimination between body-part categories

This experiment (shown in figure 2) followed the adaptation method developed by Grill-Spector and Malach (2001), but used 32 body part stimuli (similar to those used in the EBA localizer experiment) as opposed to object stimuli. Images were grayscale photographs ($12.33^\circ \times 15.81^\circ$ visual angle). Participants completed two experimental runs (counterbalanced by reversing the block order). Each run comprised of ten experimental blocks (230 volumes; TR = 2000ms; 34 axial slices; 3mm slice thickness; 64x64 inplane resolution; 3x3x3mm matrix) lasting 32s (16 volumes) and 7 fixation blocks lasting 20s (10 volumes). The experimental blocks consisted of 1, 2, 4, 8 or 32 different body part images (each block being repeated twice within each run). Images were presented for 875ms with an ISI of 125ms.

Findings from the single cell recording, brain-imaging and psychophysics literature converge to indicate that stimulus attention leads to greater neural activity and subsequently to greater adaptation (Rezec et al., 2004; Chaudhuri, 1990; Posner and Gilbert, 1999; Van Wezel and Britten, 2002). Therefore, it is possible that variations in attention across blocks could work in opposition to the current predictions. In blocks where we would predict that attention would be higher (e.g. as the number of different images increases) we are actually expecting to observe less, not more,

adaptation. Consequently, we encouraged observers to maintain consistent attention by requiring them to covertly name each object as it was presented.

INSERT FIGURE 2 HERE

Experiment 2: discrimination within body-part categories

This experiment consisted of two counterbalanced runs (260 volumes; TR = 2000ms; 34 axial slices; 3mm slice thickness; 64x64 inplane resolution; 3x3x3mm matrix) each containing 10 experimental blocks lasting 30s (15 volumes) and 11 fixation blocks lasting 20s (10 volumes). Fixation blocks were presented either side of each experimental block. The experimental blocks consisted of five types: Identical hand (one view of the same hand repeated throughout the block); Different Parts (one view of each of six different body part images); Different Hands (one view of each of six different peoples' hands); own/other (one view of the participant's own hand and one view of another individual's hand); other/other (one view of each of two unfamiliar individuals' hands). Across the own/other and other/other blocks, each 'own' hand image also served as an 'other' hand image for another participant so that what was an own/other block for one participant was an other/other block for another participant thereby holding constant across blocks the degree of difference between the hand images in these blocks. Different images were used in each block to avoid carryover across blocks of adaptation to specific individual images. We focused on hand images because they activate the EBA and are a commonly viewed body part (e.g. we observe our own hands as we conduct actions and watch others' hands as they gesture) that, consequently, should provide a particularly sensitive test of own vs other body part recognition in the EBA. Each block type was repeated twice within

each run. All images were color photographs ($12.33^{\circ} \times 15.81^{\circ}$ visual angle) and were presented for 750ms with an ISI of 250ms. All hand images were an egocentric view of the back of the hand (see figure 3). As before, participants were instructed to covertly name each stimulus in order to maintain consistent attention during the task.

INSERT FIGURE 3 HERE

fMRI Pre-processing

Data were pre-processed using 3D motion correction with sinc interpolation and corrected for slice timing and scanning order (ascending, interleaved). One participant in Experiment 1, and three in Experiment 2, needed to be removed from further analysis due to excessive head motion. Linear trend removal and a high pass filter (cutoffs: 0.0088 Hz (EBA Localizer); 0.0078 Hz (Exp. 1); 0.0083 Hz (Exp. 2)) were also applied. Functional data were aligned to a high resolution anatomical scan (1x1x1 mm matrix, 256x256 inplane resolution, TR 1900, TE 5.57) taken in the same session. This was subsequently normalized to a Talairach template (Talairach and Tournoux, 1988) and the parameters applied to the co-registered functional data. Spatial smoothing, using a 6mm FWHM Gaussian spatial filter, was then carried out in the 3D domain once the data had been aligned to the participant's 3D anatomical scan.

Preliminary Analysis

EBA localizer: region of interest definition

In both experiments a region of interest (ROI) for each participant was established in both the right and left hemispheres using the data acquired from two EBA localizer

scans. The EBA was localized in each participant by using a body minus objects contrast (Downing et al., 2001), combining the data from the two runs. The data were thresholded to $p < 0.0001$ (uncorrected for multiple comparisons) and from this the most significant voxel in both the right and left hemispheres was identified (peak EBA voxel). The location of the mean EBA peak voxels across participants are shown in table 1 for both experiments. These Talairach coordinates correspond to an area of the middle temporal gyrus in the posterior end of the temporal lobe.

INSERT TABLE 1 HERE

A number of studies have shown that the EBA is in close physical proximity to other functional areas (Downing et al., 2001; Astafiev et al., 2004; Peelen and Downing, 2005; Astafiev et al., 2005). Consequently, the EBA ROI was established by setting a very conservative 3mm^3 box centered on the peak EBA voxel to ensure that an area of maximal response to body images was localized whilst minimizing inclusion of other functional areas (cf. Downing, Wiggett and Peelen, 2007). The use of fMR-A in the experiments then enabled us to probe the functional characteristics of sub-populations of neurons within the selected voxel.

Experiment 1: discrimination between body-part categories

The timecourses from each of the two runs were extracted from the predefined ROI based upon the EBA localizer scans. Each timecourse was then shifted forwards 3 TR's (6 seconds) to reflect the delay in haemodynamic response. Next we converted the value at each time point into percentage signal change (PSC) using the average

signal of all the baseline (fixation) blocks within a run. The converted PSC data were then averaged across runs by block type (1, 2, 4, 8, 32 different images).

Experiment 2: discrimination within body-part categories

From each participant's 3mm³ ROI centered on their peak EBA voxel (established from the EBA localizer scans taken in the same session) we extracted the average timecourses for each of five block types. These data were converted to PSC using a condition-based averaging method (Brain Voyager QX; Brain Innovation, Maastricht, The Netherlands) which calculated the PSC using the fixation period preceding each block as the baseline. The converted PSC data were then averaged across runs by block type (Identical, other/other, etc.).

Statistical Analysis

Testing for the assumptions of normality was conducted to screen the data for both skewness and kurtosis prior to parametric testing. All conditions except Identical Hand, Different Hands and own/other, in the left hemisphere, for Experiment 2, showed values less than the criterion z of 3.29 ($p = 0.001$) recommended for small to moderate sample sizes (Tabachnick and Fidell, 1996). Consequently, statistical analysis was conducted using either t-tests (1-tailed due to specific predictions from previous research) for single pair wise comparisons or Analysis of Variance, to control for Type 1 errors, with post-hoc testing where multiple comparisons were made. All significant effects from the ANOVA analyses are reported.

RESULTS

Experiment 1: discrimination between body-part categories

Successful demonstration of adaptation related to repetition frequency in the EBA is an essential pre-requisite for using this technique to explore the functional role of the EBA in subsequent experiments. Consequently, the first experiment aimed to characterize the adaptation effect in the EBA.

Figure 4 shows the averaged repetition suppression results from all participants' data for blocks containing 1, 2, 4, 8 or 32 different body part images for the right and left hemispheres respectively. Data have been taken from the second half of each block (i.e. scans 9-16), after one full image cycle has occurred, because the effects of differential adaptation on the percent signal change will be most apparent during the second half of each block.

INSERT FIGURE 4 HERE

Figure 4 shows a clear decrease in percent signal change (i.e. increasing adaptation) as the number of different body part images presented within a block decreases. A 2-way ANOVA (Hemisphere [Right and Left] x Block [1, 2, 4, 8 and 32 different parts]) showed marginally greater activity in the right hemisphere ($F(1,10)=4.65$ $p=0.06$) and a significant effect of Block ($F(4,40)=5.036$, $p<0.01$). Post hoc testing showed that the 1 different part block was significantly more adapted than the 4 ($p<0.05$), 8 ($p<0.05$) and 32 ($p<0.0001$) different parts blocks. Furthermore the 2 and 4 different parts blocks were both significantly more adapted than the 32 ($p<0.05$).

Overall, these data provide clear evidence that neural populations within the EBA are susceptible to the effects of stimulus repetition in a similar way to those in the LOC (Grill-Spector et al., 1999; Grill-Spector and Malach, 2001), and that they distinguish between different body part categories.

Experiment 2: discrimination within body-part categories

The intention of this second experiment was to investigate the functional properties of the EBA. This was achieved using five conditions that examined within-category effects and recognition of one's own body parts.

Experiment 2a: representing different individuals' body parts

Figure 5 displays the percent signal change for each hemisphere's EBA on blocks in which 1 (Identical), 2 (other/other) or 6 different hands (Different Hands) were presented. It is evident that there was a clear monotonic decrease in percent signal change (increasing adaptation) as the number of different hand images in an epoch was reduced. A 2-way ANOVA (Hemisphere [Right and Left] x Block [Different Hands, other/other and Identical]) showed a main effect of Block ($F(2,22)=5.56$, $p<0.05$). Post Hoc analysis showed that the Identical and other/other blocks were significantly more adapted than the Different Hands block ($p<0.01$ & $p<0.05$ respectively). These findings show that the fMR-A effect, characterized in Experiment 1, is also evident within a single body part category (i.e. hands). The main effect of hemisphere and block by hemisphere interaction were not significant ($p=0.39$ and $p=0.16$ respectively).

INSERT FIGURE 5 HERE

Experiment 2b: recognition of own body parts

Figure 6 displays the percent signal change for blocks in which two other peoples' hands (other/other) or the participant's hand and another person's hand (own/other) were presented, for each hemisphere's EBA. There appears to be greater adaptation in the other/other block. A 2-way ANOVA (Hemisphere [Right and Left] x Block [own/other and other/other]) confirmed the statistical significance of this observation (effect of Block: $F(1,11)=10.02$, $p<0.01$) suggesting that neural populations within the EBA particularly distinguish one's own body parts. Furthermore, whilst the main effect of hemisphere was not significant ($p=0.178$) the interaction between hemisphere and block was marginally significant ($F(1,11)=4.71$ $p=0.053$) indicating a more pronounced adaptation effect in the right hemisphere.

INSERT FIGURE 6 HERE

Experiment 2: control analysis for possible effects of attention

It is possible that observers pay less attention to their own hand (due to its greater familiarity) than to others' hands. If so, then we should predict that observers may pay less attention in the own/other block of Experiment 2b, which following the earlier discussion should lead to less adaptation compared to the other/other block; exactly what we observed. However, such a general difference in attention would predict that we should see a similar pattern of adaptation in other visually responsive brain regions. The marginal interaction between hemisphere and block above argues against an explanation in terms of general differences in attention as the effect of adaptation for own/other compared to other/other tends towards being greater in the

right hemisphere. Nevertheless, to further confirm whether any effect was specific to the (right) EBA, timecourses in other regions responsive to these stimuli were examined. In particular, we extracted timecourses from early visual cortices and from the LOC (Malach et al., 1995), which arguably is positioned at a similar stage of visual processing to the EBA. Early visual cortices (V1/2) were identified by locating the most significant occipital regions in each hemisphere to all visual stimuli in the EBA localizer (body plus objects). This resulted in a cluster in the right (21, -88, 16, voxel count = 547) and left (-12, -91, 4, voxel count = 157) hemispheres most closely centered on Brodmann areas 17 and 18. Localization of the LOC was achieved using an objects minus body parts contrast (the reverse of that used to identify the EBA), which identified a region in both the right (30, -49, -5, voxel count = 304) and left (-27, -43, -11, voxel count = 383) hemispheres centered on Brodmann areas 19 and 37 and corresponding to a focus in the anterior ventromedial part of the LOC (Malach et al., 1995).

A 3-way ANOVA (Region [EBA, LOC, V1/2] x Hemisphere [Right and Left] x Block [Different Hands, Own/Other, Other/Other, Identical]) showed statistically significant main effects of Region ($F(2,22)=11.84$ $p<0.001$), Hemisphere ($F(1,11)=6.03$ $p<0.05$ and Block ($F(3,33)=8.55$ $p<0.001$). There was greater activity in the right hemisphere and post hoc analysis showed that percent signal change was greater in EBA and V1/2 than in LOC (p 's <0.001). In addition, post hoc analysis showed greater activity in the different hands block than in the other/other and identical blocks ($p<0.05$ and $p<0.0001$ respectively) and greater activity in the own/other block than in the other/other and identical blocks ($p<0.05$ and $p<0.001$ respectively). Importantly, for the present control analysis, there were statistically significant interactions between region and block ($F(6,66)=5.50$ $p<0.001$) and

between region, hemisphere and block ($F(6,66)=3.57$ $p<0.005$). These are shown in Figures 7 and 8 for comparison to Experiments 2a and 2b respectively.

INSERT FIGURE 7 HERE

Figure 7 shows that for both the left and right hemisphere of each ROI there is a decrease in percent signal change (greater adaptation) as the number of different hand images in an epoch decreased. However, this adaptation is much stronger in the right EBA. A 2-way ANOVA (Region [EBA, LOC and V1/2] x Hemisphere [Right and Left]) comparing the slopes of linear fits (shown in Fig. 7) to the data for each ROI and hemisphere confirmed this observation through a significant interaction ($F(2,22)=3.55$ $p<0.05$). Post Hoc analysis showed that the slope for the right EBA was significantly greater than for all other hemisphere and region combinations ($p's<0.05$) indicating that the right EBA is particularly sensitive to differences between exemplars of the same body part category.

INSERT FIGURE 8 (a) and (b) HERE

Figure 8 shows the percent signal change for the own/other and other/other blocks in both the early visual cortices (a) and the LOC (b) in the right and left hemispheres. Post Hoc testing showed that the percent signal change in the right EBA was greater in the own/other block than in the other/other block ($p<0.0000005$; see Fig. 6) but there was no difference ($p>0.05$) between these blocks in the left EBA, the left and right early visual cortices (Fig. 8a) or the left and right LOC (Fig. 8b). This analysis

confirms that the greater adaptation in the right EBA to other/other compared to own/other stimuli is not a general effect of differences in attention between blocks.

It is also worth noting that the present analyses provide further evidence that the right EBA in particular seems to hold less abstract representations of body parts than the left EBA. Not only is the right EBA particularly sensitive to within body-part category differences (including one's own body parts), as shown here, but also only the right EBA distinguishes between allocentric and egocentric views of body parts (Chan et al., 2004; Saxe et al., 2005).

Comparison of discrimination between body-part categories in EBA, LOC and V1/2

For interest we also identified the early visual cortices and LOC in Experiment 1 using the same contrasts as described previously for Experiment 2. For the early visual cortices, this resulted in clusters in the right (18, -88, 13, voxel count = 289) and left (-9, -94, 7, voxel count = 366) hemispheres most closely centered on Brodmann areas 17/18. For the LOC the right (30, -49, -5, voxel count = 419) and left (-27, -49, -8, voxel count = 254) clusters were centered on Brodmann areas 19/37.

A 3-way ANOVA (Region [EBA, LOC, V1/2] x Hemisphere [Right and Left] x Block [1, 2, 4, 8 and 32 different parts]) showed statistically significant main effects of Region ($F(2,20)=9.91$ $p<0.005$), Hemisphere ($F(1,10)=7.83$ $p<0.05$) and Block ($F(4,40)=14.60$ $p<0.0000005$) but no significant interactions. There was greater activity in the right hemisphere and post hoc analysis showed that percent signal change was greater in EBA and V1/2 than in LOC ($p<0.0005$ and $p<0.005$

respectively). The main effect of block can be seen plotted on log-linear axes in Figure 9.

INSERT FIGURE 9 HERE

For all regions and hemispheres percent signal change decreases (adaptation increases) as the number of different images presented in a block decreases. As would be expected, given the non-significant interactions, the slopes of logarithmic fits to the data (shown in Fig. 9) did not differ significantly ($p > 0.05$). In other words all three regions were equally sensitive to differences between body part categories. One explanation for these findings would be that some general process, such as variation in attention or repetition of the covert naming responses, underlies the adaptation effects observed causing the equivalent effects in multiple brain areas. However, the region and hemisphere specific effects observed in experiment 2 argue against this interpretation. Further, adaptation in early visual cortices and the LOC to body part images from different categories is expected. The early visual cortices will be sensitive to the local variations between the different body part images and so will adapt more as this variation reduces (i.e. in the conditions with fewer different body part images). In addition, a number of studies have shown that the LOC is selective for body part images (cf. Downing, Wigget and Peelen, 2007). Thus, it is not surprising that the LOC, like the EBA, shows increasing adaptation as the number of different between category body part images decreases. These observations also serve to further emphasize the specificity of the findings from Experiment 2. Whilst all the regions tested here are sensitive to differences between images from different body

part categories the right EBA is uniquely sensitive to differences between images *within* a body part category and to images of one's own body part in particular.

DISCUSSION

The results of the first experiment suggest that neural networks in the EBA, like those in the LOC (Grill-Spector and Malach, 2001), are sensitive to the effects of stimulus repetition (fMR-A). Further, the observation that less adaptation is observed when many different body parts are presented supports the notion that the EBA contains networks that distinguish between different body parts rather than simply responding to body parts *per se*. The within-category repetition suppression effect reported in Experiment 2a showed a similar, particularly strong, monotonic trend for adaptation in the right EBA as a function of the number of within category exemplars. This implies that networks within the right EBA are also capable of distinguishing exemplars within a single body-part category and may facilitate discrimination of identity from body part images. Peelen and Downing (2007) had previously argued that the EBA was not sensitive to identity and had instead suggested that this might be a function of the recently identified Fusiform Body Area (FBA), which is located adjacent to the Fusiform Face Area. However, it had also been argued that such subordinate, and especially expert, level visual processing might be the preserve of the Fusiform Face Area (Tarr and Gauthier, 2000). Peelen and Downing's suggestion could be accommodated by the idea that a slightly enlarged region of the fusiform gyrus incorporating both the FFA and FBA carries out subordinate level visual processing. However, the sensitivity of the right EBA to within category differences demonstrated here, by using fMR-A, refutes both the idea that the EBA is not sensitive to identity and that subordinate visual processing is the preserve of a single specialized brain area. Instead the present findings are more consistent with the idea that subordinate visual processing could be carried out in multiple, domain specific, visual areas (Kanwisher, 2000; McKone et al., 2007) including the EBA.

The strength of the present fMR-A approach is further demonstrated by the observation, in Experiment 2b, that the right EBA distinguishes images of one's own body parts from those of others. Two previous studies had shown that the right EBA is activated less by images of body parts from egocentric viewpoints than by allocentric views of body parts (Chan et al., 2004; Saxe et al., 2005). These findings appeared to suggest that the EBA helped perception of others' bodies perhaps providing important information for social cognition. The difference in activity to allocentric compared with egocentric views of body parts found in both studies also suggests that the EBA may be able to use viewpoint as an indicator of body part ownership (an allocentric view cannot be an own body part, an egocentric view could be). However, a further comparison in one of these studies (Chan et al., 2004), found no difference in EBA activation between images of oneself and images of others. The present work suggests this null finding may have been the result of a standard fMRI contrast applied within an ROI that lacked the sensitivity to the different interleaved neural populations within single voxels identified by the adaptation approach used here. The current observation that a condition which contained an image of the participant's own hand and one of some else's hand was significantly less adapted than a condition containing two unfamiliar hand images suggests that the right EBA contains distinct neural populations to process own vs. others' body part images. This capability suggests that the right EBA may play an important role in the integration of visual body part information with other modalities. For instance, psychophysical work has shown that somatosensory processing is enhanced by relevant visual information. Kennet, Taylor-Clarke and Haggard (2001) found that two-point touch discrimination thresholds were smaller when participants viewed the relevant body

site prior to stimulation. In a subsequent event-related potential study, they found that this visual information modulated the activity of neurons in somatosensory cortex areas SI and SII (Taylor-Clarke et al., 2002). The capacity of the right EBA to distinguish images of one's own body parts suggests that it is well placed to provide the necessary visual input to modulate somatosensory processing as part of a body-touch network.

In conclusion, whilst exploration of the functional significance of the EBA is in its infancy the present results suggest that in addition to recognizing others' body parts, thereby providing information for social cognition (cf. Peelen and Downing, 2007), the right EBA also plays an important role in the visual recognition of our own body parts thereby providing crucial information for integration with other sensory modalities.

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FIGURE CAPTIONS

Figure 1. One run (of two) used in the EBA Localizer runs. Blocks of 45 grayscale different body and object images were presented interspersed with shorter fixation blocks.

Figure 2 (after Grill-Spector and Malach¹⁶). Details the contents of each experimental block within one run. Each block was made up of 1, 2, 4, 8 or 32 different body part images presented twice within each run interspersed with blocks of fixation.

Figure 3. Sample stimuli from the conditions in experiment 2. (a) different hands (b) own/other (c) other/other (d) identical.

Figure 4. Experiment 1 effect of repetition suppression in the EBA of the right and left hemisphere. Both show a monotonic decrease in percent signal change as a function of the decrease in number of different images presented. Overall activity appears greater in the right hemisphere EBA. Error bars show ± 1 SE_M.

Figure 5: Effect of repetition suppression within a body-part category (Experiment 2) for each hemisphere. The percent signal changes decreases as the number of different hands shown decreases; 6 different hands (Different Hands); 2 different hands (other/other); 1 hand (Identical). Overall activity appears greater in the right hemisphere EBA (significant on a one-tailed t-test $t(11)=2.673$ $p<0.05$ but not in the ANOVA). Error bars show ± 1 SE_M.

Figure 6. Percent signal change for the own/other and other/other conditions (Experiment 2) is plotted for the right and left hemispheres. There is greater adaptation in the other/other blocks. There was a non-significant trend for greater activation in the right hemisphere. Error bars show ± 1 SE_M.

Figure 7. Percent signal change as a function of stimulus repetition within a body part category (Experiment 2) for right and left hemisphere EBA, LOC and V1/2. Number of different images values of 6, 2, and 1 correspond to the Different Hands, Other/Other and Identical blocks respectively. Linear fits to the data are shown. There is greater adaptation in the right hemisphere EBA. Error bars are omitted to improve figure clarity.

Figure 8. Experiment 2 percent signal change in the bilateral early visual processing areas (a) and ventral LOC (b). Data from both regions showed no significant differences in the degree of adaptation between own/other and other/other conditions.

Figure 9. Percent signal change as a function of number of different images (Experiment 1) for right and left hemisphere EBA, LOC and V1/2. All regions and hemispheres show, similar, increasing adaptation as the number of different images decreases. Log fits to the data are shown. Error bars are omitted to improve figure clarity.

Table 1. Mean Talairach co-ordinates of the peak EBA voxel ($\pm$ the standard deviation) in the right and left hemispheres for each experiment, located using the body minus objects EBA localizer. This corresponds to an area in the middle temporal gyrus in the posterior region of the temporal lobe.

	Right Hemisphere			Left Hemisphere		
	x	y	z	x	y	z
Exp. 1	49 $\pm$ 5mm	-64 $\pm$ 3mm	5 $\pm$ 5mm	-49 $\pm$ 7mm	-62 $\pm$ 7mm	10 $\pm$ 6mm
Exp. 2	48 $\pm$ 6mm	-63 $\pm$ 6mm	6 $\pm$ 6mm	-48 $\pm$ 4mm	-62 $\pm$ 6mm	13 $\pm$ 8mm

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8a

Figure 8b

Figure 9