The overlap of the EBA and the MT/V5 cluster

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The extrastriate body area (EBA) is located in the lateral occipito-temporal cortex, in the vicinity of the motion-sensitive region hMT/V5+. To investigate the relationship of EBA to the recently mapped retinotopic areas of the MT/V5 cluster (Kolster et al., 2010), we evaluated the proportion of voxels responsive to the presentation of static human bodies (EBA voxels) in each of the four areas of the MT/V5 cluster and neighboring LO and pFST areas. We evaluated this proportion as both a function of the number of voxels in a given area and the total number of voxels in a broader lateral occipito-temporal cortex (LOTC) ROI. We observed that each of the four retinotopic areas of the MT/V5 cluster includes substantial fractions of EBA voxels, in contrast to the LO and pFST areas. This proportion was slightly greater in the right than left hemisphere, and did not depend on the control condition. While most EBA voxels in MT/V5 were only body-sensitive, those in pMSTv and pFST were also motion-sensitive. The main locus of EBA voxels outside the MT/V5 cluster was in the LOTC cortex just rostral to the MT/V5 cluster. Although this region contained more EBA voxels than the MT/V5 cluster, the proportion as a function of areal size was much reduced compared to the MT/V5 cluster. Our results show that EBA is not a single cortical area as EBA voxels are located in all four areas of the MT/V5 cluster, and that body-sensitivity is a key feature of the MT/V5 cluster, in keeping with its exquisite sensitivity to observed actions of others.

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Introduction

There is growing evidence for category-specific processing at higher levels of the human and non-human primate visual system. In both species, regions, deemed patches or areas, specific for faces, bodies and places have been described (Agirre et al., 1998; Downing et al., 2001; Epstein and Kanwisher, 1998; Kanwisher et al., 1997; Nasr et al., 2011; Pinsk et al., 2009; Popivanov et al., 2012; Tsao et al., 2003). In humans, the extrastriate body area (EBA) was initially described as a region dedicated to the processing of visual information about other people’s nonfacial body parts (EBA, Downing et al., 2001). Since then, numerous studies have revisited this area proposing additional functional roles such as updating the representation of one’s own body after movements (Astaev et al., 2004), mapping the visual representation of another’s body onto one’s own body (Jackson et al., 2006), distinguishing between one’s own and someone else’s body parts (Jennerod, 2004) and integrating information about body shape and body movement during action observation (Jastorff and Orban, 2009). Thus, this region plays an important role in action observation/execution.

In the initial definition EBA was located above and in front of the human motion complex or hMT/V5+, but was considered a separate entity because the overlap was only partial and functional characteristics differed. However, subsequent studies using more sensitive methods observed extensive, if not complete overlap on the one hand (Jastorff and Orban, 2009; Peelen et al., 2006; Spiridon et al., 2006) or complete segregation with body part selective regions surrounding the motion-sensitive region on the other (Weiner and Grill-Spector, 2011). Hence the overlap between hMT/V5+ and EBA reported thus far, ranges from very little to complete.

However hMT/V5+ is not a single area but a complex of areas, some of which are likely to be the homologues of monkey MT/V5 and its satellites MST and FST (DeYoe et al., 1996, Huk and Heeger 2002, Kolster et al., 2010). Indeed it has recently been shown that substantial parts of hMT/V5+, in fact the posterior two thirds, are retinotopically organized (Amano et al., 2009; Kolster et al., 2010), although it was initially assumed that EBA was located outside retinotopic cortex (Downing et al., 2001). Thus contrary to initial claims, it is likely that EBA overlaps with retinotopically organized regions.

The overlap between EBA and retinotopic cortex has important consequences as to whether or not EBA is a single cortical area as was initially reported (Downing et al., 2001) and is commonly assumed (Peelen and Downing, 2007). Indeed by definition, a cortical area can only include a single retinotopic map (Allman and Kaas, 1971; Van Essen, 1985). Hence if EBA overlaps with retinotopic cortex, it can be a single cortical area only if the overlap is complete.
and EBA is coextensive with a single retinotopic map. Any other arrangement, such as incomplete overlap or overlap with several retinotopic maps, would indicate that EBA voxels belong to several cortical areas and do not define a single cortical area, implying that in fact the extrastriate body area is a misnomer. This would not need to imply that body selective voxels do not exist nor that voxels cannot be simultaneously retinotopically and body selective — even single neurons could share such properties. It would simply show that the functional characteristic of body selectivity is insufficient to unambiguously define a single cortical area. This latter possibility was our preferred alternative as growing evidence indicates that sets of neighboring areas can share a given property. This has been shown for sensitivity to motion (Kolster et al., 2010; Larsson and Heeger, 2006), to kinetic boundaries (Larsson and Heeger, 2006), to stereopsis (Georgieva et al., 2009; Preston et al., 2008) and may also apply to the body localizer. Hence the present study was undertaken to clarify the relationship between EBA and the four retinotopically defined areas of the human MT/V5 cluster and neighboring cortex.

Materials and methods

Participants

Functional magnetic resonance data were acquired from 11 healthy volunteers (5 females, 6 males, mean age 25.9 years, range 22–31 years), 7 of whom participated in the Kolster et al. (2010) study. All participants were right handed, had normal vision or corrected-to-normal vision using contact lenses; they had no history of any mental or neurological diseases. Ethical Committee of KU Leuven Medical School approved the study. Before MRI sessions, all volunteers gave their written informed consent in accordance with the Helsinki Declaration.

Participants viewed a screen positioned in the bore of a magnet at a distance of 36 cm from their eyes through a mirror tilted at 45° and attached to the head coil. Stimuli were projected with a LCD projector (Barco Reality 6400i; 1024×768; 60 Hz refresh frequency) onto the screen. Participants were asked to remain immobile while fixating a target point at the center of the screen. Eye position was recorded with an ALS eye tracking system 5000 (60 Hz, Applied science laboratories).

Stimuli and experimental design

Retinotopic mapping

Eccentricity and polar angle measurements (Sereno et al. 1995) were acquired using a procedure described in Kolster et al. (2010) as summarized below. A single experimental session consisted of 4 polar angle and 4 eccentricity runs. During each run, 128 volumes were acquired and 4 complete cycles of both expanding and rotating stimuli, each of them lasting 64 s, were presented. During a given cycle, each point of the visual field was stimulated for 8 s to maximize the amplitude of hemodynamic response. The stimuli evolved only in clockwise (polar angle) or expanding (eccentricity) direction in order to avoid a superimposition of responses in opposite directions and to allow responses to return to baseline between two consecutive cycles. Both eccentricity and polar angle stimuli consisted of black and white checkerboard pattern, counter-phase flickering at the frequency of 6 Hz and presented on a grey background, the luminance of which equaled the mean luminance of the black and white segments. The polar angle stimuli consisted of a wedge 45° in polar angle and extending from 0.25 to 7.75° in eccentricity. The wedge was composed of 4 segments in the azimuthal direction and 24 segments radially. The radial size of segments was adjusted according to the log(r) law to approximate to human magnification factor. The eccentricity stimuli consisted of expanding annuli centered on a fixation point. These comprised 24 squares in the azimuthal direction with a stepwise expanding radius. Radial size of the segments, diameter and width of the annuli were adjusted in according to log(r) law. One full expansion cycle covered a fixed eccentricity range from 0.25° to 7.75°.

Body localizer

All subjects were tested with an EBA localizer. Following Downing et al. (2007), the EBA localizer consisted of blocks in which images of headless human bodies alternating with blocks of images of chairs, using the stimuli retrieved from the Downing website, as in Jastorff and Orban (2009). Most bodies were portrayed standing, but 3 of the 20 were shown in a sitting position. Maximum extent of the body stimuli was 10° vertically and 7° horizontally, with the mean across stimuli being 9° vertically and 4° horizontally. In eight out of the 11 subjects, a second control category was included, which portrayed manmade objects, matched with the human bodies for size, luminance and aspect ratio, defined as the ratio between the first and the second Eigen vectors of the objects. Thus, the localizer runs included either three (3 subjects) or four (8 subjects) conditions, corresponding to bodies, chairs, fixation baseline and the object condition. Run (360 s) and block (30s) durations were identical for all subjects, but for the runs with three conditions, every condition was shown four times, whereas for the runs with 4 conditions, conditions were shown 3 times. In the first group of 3 subjects, who participated in Kolster et al. (2010) and Jastorff and Orban (2009), 2 runs were collected, in the second group of 8 subjects, four of which participated in Kolster et al. (2010), 3 runs were collected. Different numbers of runs were sampled to equate the number of volumes that was utilized in the body and motion contrasts (see below).

Motion localizer

All subjects were tested with 2 runs of motion localizer in which blocks of moving random texture pattern (7° in diameter) alternated with blocks of the same static pattern (Sunaert et al., 1999). Although the timing of these runs (blocks 30 s, 6 presentations per condition, runs of 360 s) was exactly the same in all 11 subjects, the number of volumes collected differed in 3 subjects, because of a different TR (see below).

Imaging data acquisition

Data were acquired with a 3 T MR scanner (Achieva; Philips Medical System). All functional images consisted of gradient-echo echoplanar images. The retinotopic functional imaging parameters were as follows: 128 volumes, 36 tilted coronal slices (2 mm thickness, 0.2 mm gap), TR of 2.0 s, 96×96 acquisition matrix (2×2 mm in plane resolution), and SENSE factor of 2.5. The parameters for the functional sessions devoted to the body and motion localizers, were 50 or 35 horizontal slices (2.5 mm slice thickness; 0.25 mm gap), time of repetition (TR) 3 or 2 s, time of echo (TE), 30 ms; flip angle, 90°; 80×80 matrix with 2.5×2.5 mm in-plane resolution, and SENSE reduction factor of 2. For the 3 subjects with 2 runs of the body localizer, the TR was 3 s and the number of slices 50. For these subjects, the total number of volumes was 240 in both localizers, amounting to 80 volumes for each condition in the body contrast and 120 for each condition in the motion contrast. For the 8 subjects with 3 runs of the body localizer, the TR was 2 s and only 35 slices were scanned. In total, 540 volumes were scanned for the body localizer (135 per condition) and 360 for the motion localizer (180 per condition). These numbers of volumes allowed for reliable identification of body- and motion responsive regions in individual subjects.

A high resolution T1-weighted image covering the entire brain was acquired for each subject (TE/TR, 4.6/9.7 ms; inversion time, 900 ms; slice thickness, 1.2 mm; 256×256 matrix; 182 coronal slices; SENSE reduction factor, 2.5).
Imaging data analysis

Segmentation and creation of nodes surface

Segmentation of anatomical volume and creation of occipital flattened surfaces were carried out in each subject by using Freesurfer tools (Fischl et al., 1999) (http://surfer.nmr.mgh.harvard.edu). Both white/grey matter and pial surfaces were segmented: white matter surface was built as last step of segmentation process and then computationally inflated, for right and left hemisphere independently. An inflated surface was reconstructed as a triangular mesh, whose vertex points (nodes) represented three-dimensional coordinates dividing white from grey matter. The occipital flattened surface was generated by first cutting off the posterior part of the inflated surface and then computationally flattening with a Freesurfer algorithm. After phase-encoded analysis, the phase information of retinotopic data was projected onto nodes, and visualized on a flattened occipital surface. In order to convert voxel to node value, three points along the normal vector of each node were defined. A value was attributed to each node by a weighted-average function, averaging values of the voxels overlapping with selected points along the normal, assigning more weight to those voxels values which showed more overlap with grey matter. The data from functional localizers were also painted onto occipital flattened surface, for visualization purpose. To this end a Freesurfer function was used, assigning to each node the maximum value amongst those voxels intercepted by the normal vector, and overlapping at least 30% with grey matter.

Definition of retinotopic areas

Right and left retinotopic maps of 7 subjects were taken from Kolster et al. (2010) study. For the remaining 4 subjects the retinotopic data were analysed in the same manner as described in that study and summarized below. All retinotopic data were motion corrected by using SPM 5 (Welcome Department of Cognitive Neurology, London, UK). Subsequently, eccentricity and polar angle data were averaged separately in two data volumes, each 128 time points in length. The volumes were smoothed with a kernel size of one-half in length. The volumes were averaged in both right and left hemispheres.

Retinotopic areas were defined first by determining the projections of central representations and eccentricity ridges, and secondly by identifying projections of meridians radiating from central representations, as described by Kolster et al. (2010). Figs. 1A and B, show the eccentricity and polar angle maps for the right hemisphere of subject Kat, one of the novel subjects not included in the Kolster et al. (2010) study. The central representation of the MT/V5 cluster is located at the same dorso-ventral level as the central confluence and it is separated from lateral occipital regions LO1 and LO2 by an eccentricity ridge (purple line), which surrounds most if not all of the MT/V5 cluster. From the central representation of this cluster, 4 vertical meridians project in directions orthogonal to the eccentricity ridge. MT/V5 extends dorsally from central representation and is bordered caudally by a lower vertical meridian and rostrally by an upper vertical meridian. In some hemispheres, lower vertical meridian is shifted rostrally so that the hemifield representation of MT/V5 is tilted in a rostral direction, as is the case with the right hemisphere displayed in Fig. 1B. MT/V5 is bordered rostrally by pMSTv, which is mirror-symmetric around the upper vertical meridian. Next to pMSTv, lies pFST, which is symmetric around the lower vertical meridian. MT/V5 is bordered on the caudal side by V4t, in which the polar map is again mirror-symmetric around the lower vertical meridian (Kolster et al., 2010). The definition of the four ROIs corresponding to these four areas was straightforward: these are circular segments with their tip in the cluster center, the relevant vertical meridian as lateral edges and the eccentricity ridge as the base (Fig. 1C). These four ROIs correspond, in principle, to eccentricities up to 7.75° which was the maximum included in the retinotopic stimuli.

The central representation of LO1 and LO2 (Georgieva et al., 2009; Kolster et al., 2010; Larsson and Heeger, 2006) is located in the rostral most part of the central confluence. LO1 extends from lower vertical meridian, which separates it from V3 dorsal and the V3A/V3B pair, to an upper vertical meridian, which represents the border with LO2. LO2 extends from an upper vertical meridian, shared with LO1, to a lower vertical meridian located more ventrally. Both LO1 and LO2 are located between the central confluence and the MT/V5 complex but separated from it by the eccentricity ridge. They are likely to be more reduced than originally described by Larsson and Heeger (2006), because of a different definition of V3A, which neighbours LO1. To define the ROIs for these two areas (Fig. 1C), we extended

Fig. 1. Retinotopic mapping of the MT/V5 cluster and neighboring retinotopic areas: LO1, LO2 and phPTd and phPTv in right hemisphere of subject Kat. A: eccentricity map, B: polar angle map and C: outlines of ROIs corresponding to the 6 retinotopic areas defined in A&B. In A, B purple lines indicate eccentricity ridges (surrounding MT/V5 cluster, surrounding phPT cluster, between V3A and V3B, between hV4 and VO); full and stippled black lines: lower and upper vertical meridians, asterisks: central visual field representations. LOS: lateral occipital sulcus, ITS: inferior temporal sulcus, OTS: occipito-temporal sulcus. Scale bar indicates 1 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the web of this article.)
the vertical meridians bordering LO1 and LO2, until they met in the rostral part of the central confluence. This meeting point defined the tip of the ROI segments, the lateral sides were the vertical meridians and the base was an iso-eccentricity line starting from the eccentricity ridge of the MT/V5 cluster and extending either dorsally towards the V3A/V3B border or ventrally to the lower vertical meridian of LO2 or its extension (Fig. 1C).

The central representation of the phPIT cluster is located below that of the MT/V5 cluster and is surrounded by an eccentricity ridge. From central representation upper and lower vertical meridians extend in caudal and rostral direction respectively, separating dorsal (phPITd) from ventral (phPITv) hemifield representations (Kolster et al., 2010). The two ROIs of this cluster were two half-ellipses (Fig. 1C) defined by the eccentricity ridge, with the vertical meridians splitting the cluster in two. LO1, LO2 and the four areas of the MT/V5 cluster were observed in all 22 hemispheres. phPITd and phPITv were also defined in all hemispheres with the exception of one right hemisphere, in which the vertical meridian projections could not be defined. In this hemisphere the cluster was arbitrary divided into dorsal and ventral halves.

The final step in this analysis was to determine the set of voxels corresponding to each ROI defined in the flatmaps. These voxels were obtained as follows. First, the sixteen ROIs were transformed to volumes with a Freesurfer algorithm employing the mean image, created by the realignment of functional volumes, as a volume template. The resulting volume of a retinotopic area corresponded to a set of voxels. Next, the voxels shared by neighbouring areas were tagged and subsequently reassigned in equal numbers to the areas sharing a border. Table 1 lists the average size of each retinotopic area as defined by the number of voxels attributed to that area. Most areas averaged between 60 and 100 voxels (Table 1), with right MT/V5 having the highest average (136 voxels) and right pFST the smallest (52 voxels).

**Definition of the lateral occipito-temporal cortex (LOTC) ROI and its subdivisions**

A right and left LOTC region of interest was defined in each subject using the following criteria (Fig. 2). A line was drawn from the center of MT/V5 cluster to the most rostral part of the circle fitted to the MT/V5 cluster boundary; this line (white in Fig. 2) was extended to a point 20 mm beyond the cluster. This point represented the most rostral part of the ROI. Next, an elliptical ROI, centered near the midpoint of the MT/V5 cluster was fitted by adjusting its height and width in such a way that the ellipse passed through the most rostral point defined in step 1 and included both phPIT and LO clusters. This definition satisfied several constraints: including the maximum number of EBA voxels while avoiding those of FBA, creating a ROI as small as possible while including all the retinotopic regions and avoiding extreme ratios of the minor and major axes of the ellipse.

Second, this LOTC ROI was partitioned into anterior, posterior and inferior subdivisions as follows. 1. A line was drawn through the MT/V5 cluster center, perpendicular to the line which in step 1 defined the anterior extent of the ellipse; this line (black stippled line if Fig. 2) extended both dorsally and ventrally up to the border of the ROI. If the lower part of the line overlapped with the phPIT cluster, it was tilted around the center of the MT/V5 cluster, so that it avoided the phPIT cluster. The part of the ROI rostral to this line was designated the anterior part. 2. A second line was drawn, which started from the center of the MT/V5 cluster and ran between the LO and phPIT clusters until it reached the caudal border of the LOTC ROI (black stippled line in Fig. 2). This line separated the posterior (above the line) from the inferior (below the line) parts of the ROI. Anterior, posterior, and inferior parts of the LOTC ROI included only regions of the ROI outside the ROIs defined retinotopically.

To calculate the probability maps of left and right LOTC, we transformed the LOTC from the individual anatomies to fs-average template in Freesurfer. The regions of various percentages of overlap across subjects were computed by selecting the nodes that were common to the required number of subjects.

**Statistical analysis of body and motion localizers**

Preprocessing and statistical analysis of body and motion localizer were carried out with SPM 5 software. Preprocessing comprised only a realignment step, where all raw images were aligned with the first image, and a mean image was created. No smoothing was performed. For each participant two different general linear models (GLM) were built in order to model onsets and durations of the two localizers, independently. For the body localizer, the design matrix was composed of 3 or 4 regressors modelling the experimental conditions: body, chair, fixation and objects if applicable, plus six regressors taken from realignment. For the motion localizer, 2 regressors modelled the motion and static conditions, plus the six regressors from the realignment. All regressors of both design matrices were convolved with the canonical hemodynamic response function. Subsequently body vs chair and motion vs static contrasts were created at the first level for each subject and the resulting t score maps were used for further analysis. Voxels reaching t = 3.1 (p < 0.001 uncorrected) in these contrasts were considered body and motion-sensitive. Body-sensitive voxels when located within LOTC were subsequently referred to as EBA voxels (see below). In 8 out of the 11 subjects, body-sensitive voxels could also be evaluated by a second contrast: body vs object.

We performed two complementary sets of analyses of the EBA voxels in individual subjects. The fixed threshold analysis investigated

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**Table 1** Average sizes (number of voxels) of the eight retinotopic areas and the 3 parts of the LOTC ROI.

<table>
<thead>
<tr>
<th></th>
<th>LO1 L</th>
<th>LO1 R</th>
<th>LO2 L</th>
<th>LO2 R</th>
<th>MT/V5 L</th>
<th>MT/V5 R</th>
<th>pMSTv L</th>
<th>pMSTv R</th>
<th>pFST L</th>
<th>pFST R</th>
<th>pVT4 L</th>
<th>pVT4 R</th>
<th>pPhITd L</th>
<th>pPhITd R</th>
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<th>Post R</th>
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<th>Inf R</th>
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</table>
The variable-threshold analysis: Analysis of the distribution of EBA voxels in the LOTC and the MT/V5 cluster

In order to characterize the distribution of EBA voxels in LOTC, including the parts of cortex outside the retinotopic areas, a second analysis was performed. The aim of this analysis was to investigate the distribution of EBA voxels across six regions of interest: the MT/V5, LO, and pMST clusters, plus the anterior, posterior and inferior parts of LOTC (Fig. 2). Because the number of EBA voxels in the LOTC ROI differed across subjects for the fixed threshold of t = 3.1 (Table 2), the 100 LOTC voxels with the highest t scores in the body contrast were selected in every individual hemisphere. 100 voxels were chosen because the number of voxels reaching the variable threshold in each subject. Consequently, we listed the number of 100MS EBA voxels subdivided the MT/V5 cluster into its four retinotopic areas (MT/V5, pMSTv, pMSTp, pFST, pV4t) and listed the number of voxels contained within each sub-part relative to the fraction of the 100MS EBA voxels in LOTC that belonged to the MT/V5 cluster. This analysis is complementary to that in the fixed threshold analysis. Results were analyzed using a one-way repeated-measure ANOVA including the four areas.

The second test investigated the spatial relationship between EBA voxels and MT/V5 cluster: whether EBA voxels were more concentrated in the central, in the middle or in the peripheral parts of the cluster. Three concentric circles, centered on the MT/V5 cluster midpoint, were drawn on the flomap, dividing the cluster and its immediate neighbourhood in two annuli (peripheral and middle), and a central circle per subject. The radius of the larger circle was chosen in a way to include the most peripheral part of the cluster. Subsequently the voxels belonging to the three parts were extracted. Because neighbouring parts (e.g. peripheral and middle annuli or middle annulus and central circle) shared some voxels, shared voxels were divided in such a way that the three parts included equal number of voxels. The number of such voxels varied considerably across subjects, (from 38 to 309 voxels, mean: 122), because it depended on the size and shape of the cluster. Within a given subject, however, the three parts differed by less than 3 voxels (median 1 voxel). Thus the number of voxels representing each part was matched within each subject. Consequently, we listed the number of 100MS EBA voxels within each concentric part and calculated the percentage relative to the fraction of the 100MS EBA voxels lying within the larger circle which included the MT/V5 cluster and its immediate neighbourhood. Results were analyzed using a one-way repeated-measure ANOVA comparing the two annuli and the central circle.

To confirm these results, all steps of this analysis, both for the LOTC ROI and the MT/V5 cluster, were repeated using the 200 most significant EBA voxels. The threshold t score defining these 200 voxels

### Table 2

<table>
<thead>
<tr>
<th>Subject</th>
<th>Total number of voxels in LOTC</th>
<th>Number of EBA voxels at fixed threshold (3.1)</th>
<th>% of EBA voxels at fixed threshold (3.1)</th>
<th>t score in local max</th>
<th>t score variable thresh (100 voxel)</th>
<th>Total EBA voxel per hemisphere</th>
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<td>L</td>
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</table>
in individual subjects ranged from 1.5 to 4.2 (mean = 2.6) for the left LOTC and from 2.3 to 5.6 (mean = 3.4) in the right LOTC.

3. Results

Before addressing the issue of the distribution of EBA voxels across retinotopic areas, we describe the lateral occipito-temporal region in which these voxels are located.

The distribution of EBA voxels in the lateral occipito-temporal cortex of single subjects

In this first section, we are investigating whether body-sensitive voxels indeed cluster around the MT/V5 complex as described previously and whether our definition of the LOTC ellipse (see Materials and methods) was able to capture a large fraction of the body-sensitive voxels within each hemisphere.

The distribution of body-sensitive voxels in the lateral occipito-temporal cortex for subject Tin is shown in Fig. 3. Note the absence of smoothing in the figure. In the right hemisphere the threshold corresponding to the 100MS EBA voxels in the LOTC ellipse equaled 4.2, slightly above the fixed threshold of \( t = 3.1 \), while in the left hemisphere the variable threshold was \( t = 2.7 \), slightly below the fixed threshold. In fact, out of a total of 155 body-sensitive voxels reaching the variable threshold in the right hemisphere (yellow nodes in Fig. 3B), 65% were well located within the LOTC ellipse, overlapping with the areas of the MT/V5 cluster as well as with the more anterior part of the ellipse, thus confirming the clustering of the body-sensitive voxels in this region. The LOTC ellipse avoided the body-sensitive voxels in the posterior part of OTs (yellow arrow in Fig. 3B) that may be considered the posterior extension of EBA. In the left hemisphere the body-sensitive voxels were also clustered in the LOTC ellipse, but, unsurprisingly given the lower threshold, more voxels were scattered throughout occipital cortex and neighboring temporal and parietal regions. In this hemisphere 257 voxels reached the \( t = 2.7 \) threshold, of which 39% were included in the LOTC ellipse. The last column of Table 2 gives the number of body-sensitive voxels in the two hemispheres for the variable \( t \) score defining 100 EBA voxels in the LOTC ellipse. The average values of 228 and 161 voxels in the left and right hemispheres are close to the values of subject Tin (257 and 155), making this individual a representative subject.

Fig. 4 illustrates the range of clustering of body-sensitive voxels for the right hemisphere. Clustering was very tight in subjects And and Kat, for whom 76% and 82% of the body-sensitive voxels of the hemisphere were located in the LOTC ellipse. Subject Ing illustrates the opposite end of the spectrum, with only 51% of the body-sensitive voxels of the hemisphere within the LOTC ellipse. Yet clustering was still evident even here. The latter figure also indicates that most of the remaining voxels outside the ellipse were located near its anterior tip (arrow in Fig. 4C), as was the case in the right hemisphere of Tin. The spectrum shown in Fig. 4 is representative of the right hemisphere, insofar as subjects Kat and Ing were respectively those having the least and most body-sensitive voxels at variable threshold located outside the LOTC ellipse. In the left hemisphere, such voxels were more frequently located outside the ellipse: in 5 subjects, including subject Tin (Fig. 3A), the proportion of variable threshold body-sensitive voxels within the LOTC ellipse fell below 50%, the extreme being subject And with 25%. These data clearly demonstrate that although there were varying degrees of scatter amongst body-sensitive voxels, these voxels were consistently clustered within the LOTC ellipse.

The LOTC regions in left and right hemispheres

The LOTC ellipse was defined in each of the 22 hemispheres independently and across the hemispheres the size of this ROI varied considerably, ranging from 904 voxels to 2822 voxels (mean = 1888 voxels) in the left hemisphere, and from 970 voxels to 2716 voxels (mean = 1872) in the right hemisphere (Table 2). Despite this almost threefold variation in size, the average size of LOTC was very similar in the two hemispheres, corresponding roughly to a region 60 by 30 voxels i.e. 120 by 60 mm on the flattened surface. In addition, LOTC positions overlapped considerably across subjects. In fact the LOTC region common to all 11 subjects (Fig. 5) included both banks of the ITS and MTG in the left hemisphere, and the fundus and upper/anterior bank of ITS plus MTG in the right hemisphere. Thus there is tendency for the left LOTC ellipse to be slightly more posterior than the right. A similar tendency is also observed in the local maxima reported in the literature for left and right EBA (Table 3). Interestingly, nearly all local maxima reported in earlier studies were included in the region common to the LOTC of the 11 subjects (Fig. 5, yellow numbers). Thus, the LOTC region encompassed not only most if not all of the EBA cluster of body-sensitive voxels in the individual subjects participating in the present study, but also enclosed most of the EBA regions defined in other studies, particularly those using the same stimuli (headless bodies vs chairs) as those in the present study. This justifies the use of the term EBA voxels for the body-sensitive voxels belonging to LOTC.

The local maxima for the body localizer in the LOTC ellipse of individual subjects (Table 2) ranged from \( t = 7.2 \) to \( t = 21.8 \) in the left hemisphere (mean \( t = 12.5 \)) and from \( t = 6.9 \) to \( t = 21.8 \) in the right hemisphere (mean \( t = 13.1 \)). Thus the EBA regions of the two hemispheres reached equally significant levels of activation. Yet if one were to use the number of LOTC voxels reaching a fixed threshold of \( t = 3.1 \) in the body localizer, the number of EBA voxels, and hence also the proportion of EBA voxels would be greater in the right than the left hemisphere. Number of voxels ranged from 40 to 287 voxels (mean 147 voxels) in the left hemisphere and from 109 to 450 voxels in the right (mean 231 voxels). The proportion of EBA voxels with respect to the total number of voxels within the LOTC ellipse (at \( t = 3.1 \) threshold) averaged 8.1% in the left hemisphere and 13.7% in the right (Table 2). The difference in number of EBA voxels was significant (t test) at uncorrected level (\( t = 2.08 \), \( p < 0.05 \)), the difference in percentage of EBA voxels was significant after correction for four tests (\( t = 2.54 \), \( p < 0.01 \)), indicating that the EBA region is more extensive in the right hemisphere than the left by 60–70%.

Now that we have shown that the LOTC ellipse includes most if not all of what is generally referred to as EBA, and have described the general properties of this region, we can turn to the heart of our study, the overlap of EBA with the retinotopically defined areas of the MT/V5 cluster.

Which retinotopic areas contain EBA voxels?

To address the question of which retinotopic areas contain EBA voxels, we used a fixed threshold analysis (see Methods). Figs. 3 and 4A, using variable thresholds close to the fixed threshold of \( t = 3.1 \), showed that many EBA voxels were located in the MT/V5 cluster. In most of the hemispheres shown, few EBA voxels appeared in the LO or the pITd areas, with the exception of the right hemisphere of Tin, in which EBA voxels were found in pITd. These single-subject results were confirmed by the analysis across the group of subjects.

The average percentages of body-sensitive voxels in the eight retinotopic areas of the two hemispheres are plotted in Fig. 6. Plainly, the proportion of EBA voxels with respect to the total number of voxels within a given area was larger in the MT/V5 cluster than outside the cluster and there was an asymmetry favoring the right hemisphere. The proportion of EBA voxels hovered around 15–20% in the left MT/V5 cluster and between 20 and 40% in the right MT/V5 cluster, reaching 40% in right pMSTv. These percentages are likely to be underestimates, as the size of the body stimuli was smaller than the eccentricity range used to define the retinotopic ROIs (see methods). The ANOVA analysis confirmed these observations: the factor area...
was significant ($F_{7,70} = 17.64, p < 10^{-7}$), as well as the factor hemisphere ($F_{1,10} = 11.38, p < 0.007$) and their interaction ($F_{7,70} = 3.69, p < 0.001$), indicating that the predominance of the MT/V5 cluster was stronger in the right hemisphere. Post-hoc testing indicated that in both hemispheres the proportion of EBA voxels was significantly larger in each of the four areas of the MT/V5 cluster than in each of the other four areas. In addition, the proportion of EBA voxels was significantly larger in pMSTv and pFST of the right hemisphere than the left (all Fisher LSD corrected at $p < 0.05$).

Eight of the eleven subjects were also scanned with an additional control condition, in which objects were shown, matched for size, luminance and aspect ratio to the human bodies. To verify that the results do not depend on the exact control condition, we performed the same analysis in the group of these eight subjects, defining the EBA voxels by contrasting bodies to the object control condition, rather than the chair control. As shown in Fig. 7, the results were very similar. The percentage of EBA voxels was much higher in the areas of the MT/V5 cluster, and the percentage was larger in the right hemisphere than the left, although overall percentages were slightly lower than in Fig. 6. Again the ANOVA analysis revealed significant effects of area ($F_{7,49} = 11.67, p < 2.10^{-4}$), and hemisphere ($F_{1,7} = 9.42, p < 0.02$) and a significant interaction ($F_{7,49} = 4.28, p < 0.001$). Post hoc tests demonstrated that the percentage in each of the four areas of the MT/V5 cluster exceeded that in each of the four other areas in the right hemisphere. In the left hemisphere, each of the four areas of the MT/V5 cluster contained a higher proportion of EBA voxels than each of the phPITs, and MT/V5 and V4t displayed a higher proportion than each of the LO areas. In addition, the difference in proportion of EBA voxels in left and right MT/V5, pMSTv and pFST was significant. These observations indicate the

![Fig. 3](image-url)  
Unsmoothed SPM plotting the voxels (yellow) reaching the t score in the body localizer corresponding to the 100 most significant LOTC voxels, shown on flatmaps of posterior parts of left and right hemispheres of subject Tin. Left: threshold $t = 2.7$, 100/257 = 39% of significant voxels in LOTC; right: threshold $t = 4.2$, 100/155 = 65% of voxels in LOTC. Blue outline: LOTC and subdivisions; white outlines: three clusters: 1: MT/V5, 2: phPIT and 3: LO. (For interpretation of the references to color in this figure legend, the reader is referred to the web of this article.)

![Fig. 4](image-url)  
Unsmoothed SPM plotting the voxels (yellow) reaching the t score in the body localizer corresponding to the 100 most significant LOTC voxels, shown on flatmaps of posterior parts of right hemispheres of subjects And (A), Kat (same subject as Figs. 1 and 2, B), and Ing (C). t score and % voxels in LOTC: 3.1 (A), 6.6 (B) and 6.1 (C), 76% (A), 82% (B) and 51% (C). (For interpretation of the references to color in this figure legend, the reader is referred to the web of this article.)
generality of our results, in that they did not depend on the control condition.

Is the nature of EBA voxels the same nature in the different areas of the MT/V5 cluster?

Figs. 6 and 7 demonstrated that EBA voxels were found predominantly in the MT/V5 cluster, but not in the LO or pPIT areas, despite the fact that these latter ones are shape sensitive (Kolster et al., 2010). Our next question was whether these voxels were functionally the same in all four areas of the MT/V5 cluster. Fig. 8 provides an answer: subdividing EBA voxels into body- and bi-selective voxels, yielded differing proportions of these two types of voxels in most of the four areas of the MT/V5 cluster, at least in the right hemisphere where proportions were high (Fig. 6). The previous analysis showed that just less than 30% of the MT/V5 voxels were body-sensitive (Fig. 6). Fig. 8 shows that the majority of these were also body selective, meaning, they responded strongly to body stimuli and only weakly to motion stimuli, whereas a small percentage were bi-selective, responding to bodies and motion. The small % of unaccounted EBA voxels were those excluded from this analysis, because their response to motion ranged between \( p > 0.001 \) and \( p < 0.05 \) (see Materials and methods). Interestingly, the ratio between body- and bi-selective voxels was reversed in right pMSTv and pFST compared to right MT/V5. A three-way ANOVA with the factors area, hemisphere and type of voxels, supported these observations. Although the main effect of area \( (F_{3,30} = 2.2, p=0.1) \) was not significant, that of hemisphere was \( (F_{1,10} = 8.35, p<0.02) \) confirming the data of Fig. 3. The main effect of voxel type was also significant \( (F_{1,10} = 6.08, p<0.05) \) indicating that overall there were more bi-selective voxels in the MT/V5 cluster, in agreement with the motion-sensitivity of the cluster (Kolster et al., 2010). The interaction area × hemisphere was significant \( (F_{3,30} = 5.37, p<0.005) \), but more importantly the interaction type of voxels × area was also significant \( (F_{3,30} = 9.05, p=2.10^{-4}) \). Thus the distribution of the two types of voxels differed across areas. As the three way interaction did not reach significance \( (F_{3,30} = 2.39, p=0.09) \), this was a general finding for the two hemispheres. Post hoc testing showed that in right pMSTv and right pFST the proportion of bi-selective voxels was significantly larger than that of only body-selective voxels. In right MT/V5 the opposite was true. This implies that a fraction of MT/V5 voxels were not sensitive to motion. In this respect one has to remember that here MT/V5 is defined retinotopically, and not by a motion localizer typically used to locate hMT/V5 + (DeYoe et al., 1996). Retinotopically defined MT/V5 is motion sensitive as shown in Fig. 14 of Kolster et al. (2010), but this does not imply that all MT/V5 voxels are motion sensitive in individual subjects, see Fig. 12 of Kolster et al. (2010).

The results of Fig. 7 were obtained using all the voxels attributed to a retinotopic area, including those overlapping with borders between areas and reassigned to each of the areas sharing a given border. To investigate whether these results were affected by this reassignment procedure, we reanalyzed to data after excluding the reassigned voxels. Although the power of the analysis was somewhat reduced by the smaller number of voxels, results were remarkably similar. In particular, the interaction area-voxel remained significant \( (F_{3,30} = 8.04, p<0.0005) \) and the post hoc tests comparing proportions of body- and bi-selective

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**Table 3**

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wEBA: whole body EBA.
voxels in right MT/V5, pMSTv and pFST remained significant. Thus the results of Fig. 7 did not depend on inclusion of the reassigned voxels in the analysis.

Very similar results were also obtained using the contrast bodies vs objects in 8 subjects, as shown in Fig. 9. Again, the main effect of hemisphere was significant ($F_{1,7} = 7.87$, $p < 0.05$), as were the two interactions voxels by area ($F_{3,21} = 5.35$, $p < 0.01$) and area by hemisphere ($F_{3,21} = 4.96$, $p < 0.01$). Post hoc tests showed that the proportion of bi-selective voxels was significantly larger in right pMSTv whereas the one of only body-selective voxels was larger in right MT/V5. This analysis confirmed the generality of the findings, as it did demonstrate little dependence on the control condition.

**Are the EBA voxels of the MT/V5 cluster a substantial fraction of all EBA voxels?**

The fixed threshold analysis showed that a considerable number of voxels within the MT cluster was body-sensitive, many more than in the LOs or PIts. However, it may be that these voxels represent only a small fraction of all EBA voxels located in the lateral occipito-temporal cortex and that what has been described thus far is a mere epiphenomenon. Although the proportions of EBA voxels within areas of the MT/V5 cluster, shown in Fig. 6, were far from negligible, that figure fails short of answering this question. Therefore, we performed a second, variable threshold analysis, considering a fixed number of EBA voxels in the LOTC of each subject, by adapting the threshold and taking the 100 most significant (100MS) EBA voxels in the LOTC ROI per individual hemisphere (see Materials and methods and Table 2).

The distribution of these 100 voxels across the different parts of the right LOTC ellipse is plotted in Fig. 10B. Nearly half of the EBA voxels are located in the MT/V5 cluster, with most of the remaining voxels located in the rostral part of the LOTC ellipse. Proportions are negligible in the LO and pPIT areas, but also very small in the other two parts of the LOTC ellipse. Not surprisingly the observed number of EBA voxels in the different parts of the LOTC ellipse was significantly different from the expected number based on the size of each sub-part ($\chi^2 = 89$, $p < 10^{-5}$; $df = 5$). Whereas the MT/V5 cluster and the rostral part of the LOTC ellipse contained more EBA voxels than what would have been expected given the size of the region (MT/V5 cluster: observed 44%, expected 16% in accordance with the generality of the findings, as it did demonstrate little dependence on the control condition. However, it may be that these voxels represent only a small fraction of all EBA voxels located in the lateral occipito-temporal cortex and that what has been described thus far is a mere epiphenomenon. Although the proportions of EBA voxels within areas of the MT/V5 cluster, shown in Fig. 6, were far from negligible, figure fails short of answering this question. Therefore, we performed a second, variable threshold analysis, considering a fixed number of EBA voxels in the LOTC of each subject, by adapting the threshold and taking the 100 most significant (100MS) EBA voxels in the LOTC ROI per individual hemisphere (see Materials and methods and Table 2).

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The same was true for the left hemisphere. Also here, the difference between observed and expected number of EBA voxels was very significant (100MS analysis: $\chi^2 = 58$, $p < 10^{-5}$; MT/V5 cluster: observed: 28%; expected: 14%; antiLOTc: observed: 50%; expected: 34%; 200MS analysis: $\chi^2 = 58$, $p < 10^{-5}$; all $df = 5$) (Figs. 10AC). Comparing the results between hemispheres, the number of EBA voxels within the MT/V5 cluster was significantly lower in the left (100MS: $t(11) = 2.5$, $p = 0.05$; 200MS: $t(11) = 2.8$, $p = 0.01$) whereas the one for antiLOTc stayed constant (100MS: $t(11) = 0.8$, $p = 0.4$; 200MS: $t(11) = 1.3$, $p = 0.22$). These analyses show that the MT/V5 cluster contained a larger fraction of the EBA voxels in the right than the left hemisphere, confirming the asymmetry documented with the fixed threshold analysis in Figs. 6–9. It suggests that most of the hemispheric asymmetry observed within LOTC as a whole was due to the asymmetry in the MT/V5 cluster with respect to body-sensitivity.

Given that a large fraction of the most significant body-sensitive voxels were located in the LOTC ellipses (Table 2), it is not surprising that the global maximum of the body localizer in each hemisphere was located in LOTC. There was but one exception, in the right hemisphere of subject Ing (Fig. 4C), where the global maximum was located in the posterior/inferior bank of the STS, just anterior to LOTC. This global maximum was only marginally larger ($t = 13.3$) than the local maximum of LOTC ($t = 13$), located in the MT/V5 cluster. In both hemispheres the local maximum within LOTC was most frequently
Fig. 8. Percentage of only body-selective and bi-selective voxels in the 4 areas of left and right MT/V5 cluster. Subdivisions of EBA voxels defined by fixed threshold ($t = 3.1$) in the standard contrast bodies vs chairs in all 11 subjects. Asterisks indicate significant differences in post hoc tests.

Fig. 9. Percentage of only body-selective and bi-selective voxels in the 4 areas of left and right MT/V5 cluster. Subdivisions of EBA voxels defined by fixed threshold ($t = 3.1$) in the contrast bodies vs objects in 8 subjects. Same conventions as Fig. 8.
located in the MT/V5 cluster (7/11 on the right and 5/11 on the left),
followed by the anterior part of LOTC (2/11 on the right and 4/11 on
the left); posterior part of LOTC (1/11 on the right and 2/11 on the left)
and inferior part (1/11 on the right and 0/11 on the left). These
distributions fit well with that of the local maxima of EBA reported
in other studies (Fig. 5).

Fig. 10 suggests that the anterior LOTC region included many EBA
voxels (about half). Yet LOTC is a relatively extended region. Using
the fixed threshold of 3.1 used in Figs. 6 and 7 we calculated the proportion
of only body-selective and bi-selective voxels in anterior LOTC with
respect to the total number of voxels contained in this region, analogous
to the fixed threshold analysis for the eight retinotopic areas. Proportions
were relatively modest: only body-selective: 4 and 9% in left and
right hemisphere, and bi-selective: 4 and 7% in left and right hemi-
sphere. These proportions are clearly smaller than those in the MT/V5
cluster (Fig. 6). A two-way ANOVA showed that only the main effect
of hemisphere was significant (F1,10 = 17.73, p < 0.002), not the main
effect of voxel type, nor the interaction.

In which part of the MT/V5 cluster are most EBA voxels located?

Fig. 10 showed that nearly 50% of the EBA voxels are located in the
right MT/V5 cluster and around 30% in the left MT/V5 cluster. Figs. 6
and 7 suggested that these voxels are more or less equally distributed
across the four areas. This is not necessarily the case however,
because the number of EBA voxels in these figures was expressed as
a function of the total number of voxels in each area, thus removing
the effect of area size. Therefore, in the following analysis we calculat-
ed the ratio of EBA voxels in each of the four areas of the MT/V5 cluster
with respect to the total number of EBA voxels located within the
cluster at the variable threshold for 100 and 200 voxels. Since MT/V5
is the largest area of the cluster (Kolster et al., 2010) it should include
more EBA voxels than any other area of the cluster. This was indeed
the case, as shown in Figs. 11A–D for the left and right MT/V5 cluster.
However the effect was much stronger in the right than the left hemi-
sphere. In both instances (100 and 200 voxels) most EBA voxels of the
MT/V5 cluster, over 40%, were located in MT/V5 proper, and the least,
about 15% in V4t. A repeated measures ANOVA showed that the effect
of area was significant (F3,30 = 4.6 p < 0.01 for 100 voxels and F1,30 =
6.82 p < 0.002 for 200 voxels), indicating that the voxels were differently
distributed amongst areas. Post hoc tests indicated that the proportion in
MT/V5 was significantly larger compared to pFST (p < 0.01 for 100 voxels
and p < 0.002 for 200 voxels) or to pV4t (p < 0.002 for 100 and p < 10−4 for
200 voxels). In addition, for 200 voxels, the proportion in MT/V5 was also
larger than that in p MSTv (p < 0.02) Although a similar trend was present
in the left hemisphere the ANOVAs turned out non-significant, even for
200 voxels (F3,30 = 2.04, p = 0.13). This result was most probably due
to the fact that, in contrast to the right hemisphere, MT/V5 in the left
hemisphere was similar in size to p MSTv or pFST (Table 1). These data
indicates that the asymmetry with respect to body-sensitivity in the
MT/V5 cluster was primarily one of MT/V5 proper.

The distribution across areas considers the polar distribution of the
EBA voxels within the MT/V5 cluster. The alternative distribution
in the cluster, the radial one, is interesting in view of an earlier study,
proposing that the EBA voxels occupy an annular region surrounding
the hMT/V5+ localizer (Weiner and Grill-Spector, 2011). One would
therefore expect the proportion of EBA voxels to increase radially.
Figs. 11E–H show that this is not the case, neither for the 100 most
significant voxels (Figs. 11E,F), nor for 200 (Figs. 11G,H), indepen-
dently of the hemisphere. On the contrary in all four tests, the propor-
tion of EBA voxels is the highest in the center of the MT/V5 cluster,
where the proportion approached 40%. Although the proportion sys-
tematically decreased with eccentricity, this trend was not significant,
coming closest to significance (F2,20 = 3.01, p = 0.07) for 200 voxels in
the right hemisphere (Fig. 11H). One should note that a decrease is
expected given the size of the body stimuli compared to the eccen-
tricity used to define the retinotopic ROIs. The decrease will however
be smaller than expected on the basis of stimulus size, given the
population RFs sizes in the areas of the MT/V5 cluster, which induce
a response in more peripheral parts of the retinotopic areas as docu-
mented in Fig. 13 of Kolster et al. (2010). Hence it is unlikely that the
absence of radial increase in Fig. 11 simply reflects the smaller size of
the body stimuli compared to the eccentricity range used in the
retinotopic mapping. It is worth noting that the body stimuli of the

![Fig. 10. Distributions of the 100 (A, B) and 200 (C, D) most significant EBA voxels in left (A, C) and right (B, D) LOTC. Color code indicates parts of LOTC. (For interpretation of the references to color in this figure legend, the reader is referred to the web of this article.)](image-url)
Discussion

The present results show that a very substantial fraction (25–40%, Fig. 9) of EBA voxels are located in the MT/V5 cluster. They occur in all four areas of the cluster, but predominate in MT/V5 itself. The fraction of EBA voxels is larger in the right MT/V5 cluster than the left. The majority of the remaining EBA voxels were located in the anterior part of LOTC, which is also right biased. While MT/V5 includes more only body-selective voxels, pMSTv and FST include more bi-selective voxels.

Spatial relation between EBA and the MT/V5 cluster

Our results indicate that a substantial fraction of the EBA voxels is located in the MT/V5 cluster. Downing et al. (2001) initially reported a restricted overlap between the motion localizer (hMT/V5+) and EBA. Since the MT/V5 cluster occupies only the posterior 2/3 of hMT/V5+, it was conceivable that EBA was distinct from the cluster, a view not supported by the present results. Several authors (Jastorff and Orban, 2009; Peelen et al., 2006; Spiridon et al., 2006) have reported that functional activation of the ITS region by motion and bodies occurred in overlapping but largely distinct voxels. Since these voxels were not claimed to be spatially segregated, these reports are compatible with the present results.

On the other hand Weiner and Grill-Spector (2011) recently reported segregation between the motion localizer and EBA, whereby the EBA voxels surrounded the motion activation (Fig. 12). Two important differences in the experimental procedures, however, readily explain these contradictory results. First, the motion localizer was defined using moving circular gratings rather than translating random dot patterns (RDP) used here. This elicits a very small activation (Fig. 12A), which occupies only part of the area TO1. The eccentricity map presented in that study actually shows that the motion localizer of Weiner and Grill-Spector (2011, black outline in Fig. 12) is much smaller than the MT/V5 cluster (red in Fig. 12B), the definition of which is based largely on the eccentricity ridge (Kolster et al., 2010). Since the MT/V5 cluster is smaller than the motion localizer defined by moving RDP (Amano et al., 2009; Kolster et al., 2010), the motion localizer defined by gratings is very much smaller than that defined by moving RDP. Notice also that a large part of the EBA defined by Weiner and Grill-Spector (2011), certainly its anterior and inferior parts, would fall within the MT/V5 cluster defined by the eccentricity ridge (Fig. 12, red outline).

The second difference is that EBA voxels were defined by comparing images of body parts with objects, not headless bodies with chairs. Based on tests in a few subjects, Weiner and Grill-Spector...
(2011) suggested that the activations by body parts and whole bodies were similar, in agreement with the initial observations of Downing et al. (2001). Yet a recent investigation of the occipito-temporal cortex activated by viewing body parts (Orlov et al., 2010) suggests that these regions are more extensive than the EBA localized by whole bodies (by a factor 2–3 according to Fig. 3 of Orlov et al., 2010). Furthermore the results of Kolster et al. (2010) show that LO and phPIT areas respond vigorously to static hands, suggesting that isolated body parts also activate parts of the LOC. Thus, these profound stimulus differences may explain how the two studies reach almost opposite conclusions with respect to the relative location of the MT/V5 cluster and EBA voxels, or the proximity of EBA voxels and the motion localizer.

Both studies (Weiner and Grill-Spector, 2011 and present one), however, are in perfect agreement regarding the main message conveyed: EBA is not a single cortical area. The present study shows that a substantial fraction of its voxels resides in at least four different retinotopically defined areas. Which area the voxels in the anterior part of LOTC belong to, must await further investigation and more advanced techniques (Saygin and Sereno, 2008), but in all likelihood these areas will prove distinct from those four already identified. Thus, our results support the proposition listed in the introduction, that EBA is a complex of cortical areas. Recently similar observations have been made for the place areas PPA (Arcaro et al., 2009) and TOS (Nasr et al., 2011).

Dealing with fMRI data, we cannot distinguish whether or not the same neural population within a voxel codes body selectivity and retinotopic position or whether this information is carried by a single population. Along the same line, biselective voxels, responding to both body shape and motion, could contain separate neural populations coding motion and body shape, or one population coding both. While further studies are needed to differentiate between these possibilities, the outcome will not affect our conclusion, as by definition, a cortical area can only include a single retinotopic map (Allman and Kaas, 1971; Van Essen, 1985).

It is highly unlikely that the conclusions depend upon the small uncertainties that may surround the definition of the retinotopic areas in the present study. Indeed the definition of the center of the MT/V5 cluster is very robust, as is the subdivision in four areas by varying the polar angle (Amano et al., 2009; Kolster et al., 2010, present study). The most difficult issue concerning the definitions of the four areas within the MT/V5 cluster is the exact location of the eccentricity ring defining their outer boundaries. But Fig. 11 shows that the proportion of EBA voxels depends minimally on eccentricity and that most occur in the better-defined central parts. With respect to the LO and phPIT areas small uncertainties regarding their exact extents necessarily have little effect, since the proportion of EBA voxels are equally low in the LO and phPIT clusters as in the parts of LOTC surrounding them.

**MT/V5 cluster areas are body-sensitive**

Our results show that all four areas of the MT/V5 cluster in both hemispheres are body-sensitive, a functional property that distinguishes them from neighboring areas of LO and phPIT clusters. Kolster et al. (2010) found that all areas of MT/V5 cluster are both motion and human-action sensitive, although the latter property was more clearly present in MT/V5 and pMSTv than the other two areas. These two dynamic sensitivities clearly distinguished the MT/V5 cluster from neighboring LO and phPIT areas. They also showed that pFST and pV4t are shape sensitive, as were LO2 and the phPITs, in agreement with earlier results of Kourtzi and Kanwisher (2000). Thus, the three main functional properties that distinguish the human MT/V5 cluster from neighboring areas are motion, human-action and body sensitivity, not shape sensitivity.

The combined motion and body sensitivity of the MT/V5 cluster seems at odds with the traditional view that MT/V5 is involved in processing of motion but not shape, based on monkey single cell studies (Albright, 1984; Zeki, 1974). However, motion and body shape define human actions to which the MT/V5 cluster is very sensitive. The view that body and motion-sensitivities are combined to yield action sensitivity is supported by recent studies of biological motion, showing that shape and motion cues are integrated at level of the EBA (Jastorff and Orban, 2009). Thus, the integration of shape and motion cues, during processing of biological motion and observed actions in general, might be one of the operations carried out by neuronal populations present in MT/V5 areas (Gilaie-Dotan et al., 2011; for other EBA functions, see Peelen and Downing, 2007).

**Comparison with the monkey**

Body patches recently have been reported to overlap with motion-sensitive regions in STS of the monkey (Jastorff et al., 2012); a small posterior patch overlapped with MT/V5, a middle patch with LST. We suggest that these posterior and middle patches in the monkey could be the counterpart of the two groups of the EBA voxels that we have documented in the MT/V5 cluster and anterior LOTC. Indeed LST, with which the middle patch overlaps, is located immediately in front of FST (Nelissen et al., 2006) and thus of the MT/V5 cluster. The anterior part of LOTC is located in front of the MT/V5 cluster and largely overlaps with the human motion localizer, and thus shares three functional (body-sensitivity, motion-sensitivity and integration of motion and shape cues of BM) and topological properties with the middle body patch. This view complements that of Pinks et al. (2008) who proposed that the anterior body patch of the monkey may correspond to the FBA in humans.

The association of body and motion-sensitivity in the monkey MT/V5 cluster suggests that this cluster, like its human counterpart, is involved in integrating motion and body shape for the extraction of action signals.
Indeed, monkey MT/V5 and satellites are also very sensitive to observed actions (Nelissen et al., 2006). This function seems to be enhanced in humans probably because interactions and communication with conspecifics are more important to humans. This view is supported by the expansion of body-sensitivity in the human MT/V5 cluster, particularly of the right hemisphere, compared to its monkey counterpart. This process may be facilitated by the presence of an additional motion-sensitive area in the humans: V3A (Tootell et al., 1997), allowing the functions of monkeys MT/V5 and its satellites to be distributed across the human MT/V5 cluster and V3A. Since simpler aspects of motion processing such as speed processing were taken over by V3A (Lebranche et al., 2010), the more complex function of action processing could be enhanced in the MT/V5 cluster by making it more body-sensitive.

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