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Large-Scale Mirror-Symmetry Organization of Human Occipito-Temporal Object Areas

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Summary

We have combined functional maps of retinotopy (eccentricity and meridian mapping), object category, and motion in a group of subjects to explore the large-scale topography of higher-order object areas. Our results reveal seven consistent category-related entities situated in the occipito-temporal cortex adjoining early visual areas. These include two face-related regions, three object-related regions, and two building-related regions. Interestingly, this complex category-related pattern is organized in a large-scale dorso-ventral mirror symmetry *of object category*. Furthermore, correlating this pattern to the map of visual field eccentricity, we found that the entire network of areas could be related to a single and unified eccentricity map. We hypothesize that this large-scale organization points to a possible development of high-order object areas through extension and specialization of a single proto-representation.

Introduction

The mapping of the primate visual cortex has been characterized by a continuous process of increasing parcellation and the discovery of new cortical subdivisions and areas. This process has culminated in the delineation of more than 32 different visual areas in the macaque visual cortex, including at least 14 nonretinotopic areas such as V4 transition, the floor of the superior temporal (FST) cortex, six subdivisions of the inferior-temporal (IT) cortex, and two subdivisions of the superior-temporal cortex, as well as the medially located TF and TH regions (for detailed review see Felleman and Van Essen, 1991).

However, in parallel with this wealth of distinct entities, it was noted that certain organizing principles unite the numerous visual areas into a more global organization. Particularly important for the present study is the finding that within early retinotopic cortex of the macaque, iso-eccentricity lines, i.e., regions that represent similar distances from the fovea, are organized in a continuous fashion, so that they cross smoothly and uninterruptedly through visual area boundaries.

With the advent of noninvasive imaging of the human cortex, a similar trend was observed in the study of human visual areas. This research first delineated the borders of early retinotopic areas as well as intermediate ones (Hadjikhani et al., 1998; Press et al., 2001; Tootell and Hadjikhani, 2001; Tootell et al., 1995). However, the trend for increased parcellation of the visual cortex has been most pronounced in high-order object areas. The cortex showing preferential object-related activations, found anteriorly to retinotopic cortex and posteriorly to area MT/V5, was originally termed the lateral occipital complex (LOC; Malach et al., 1995). More recently, this cortex was subdivided into a more dorsal region (lateral-occipital region [LO]) and a more ventral region (the posterior fusiform gyrus [pFs]; Grill-Spector et al., 1999).

Following these initial studies, a large number of additions and parcellations were found in the occipito-temporal cortex, mainly through mapping of differential activation patterns to specific object categories. These include buildings and scenes (Aguirre et al., 1998; Epstein and Kanwisher, 1998; Maguire et al., 1998), found in the collateral sulcus (CoS) and parahipocampal gyrus (PHG) (outside the LOC); faces (Halgren et al., 1999; Hasson et al., 2001; Haxby et al., 2000; Ishai et al., 1999; Kanwisher et al., 1997), found in the pFs; as well as activation patterns to other categories such as animals (Maguire et al., 2001; Tong et al., 2000), chairs (Ishai et al., 1999), cars (Halgren et al., 1999), tools (Chao et al., 1999), letters and words (Fiez and Petersen, 1998; Hasson et al., 2002; Puce et al., 1996), and more recently, human body parts (Downing et al., 2001).

Thus, one may conclude that as our understanding of the human object cortex grows, so will the number of distinct functional areas. However, as in macaque cortex, careful analysis of the data reveals that many specialized cortical regions, which appear to be distinct, can actually be unified within the framework of a simpler, more global topography. An example of such "unification" was reported recently, with the finding that the functionally and anatomically distinct building- and face-related activations, within the ventral occipito-temporal (VOT) cortex appear to be parts of a more global map of visual field eccentricity (Levy et al., 2001). This eccentricity map forms a topographic extension of the center-periphery organization found in early retinotopic cortex. Given these findings, we hypothesized that the object-related localization might reflect differences in the resolution needs of different recognition processes. Indeed, in a subsequent experiment, we have found that letter strings and words, whose recognition largely depends on foveal vision, were also mapped mainly within the left center-biased representation (Hasson et al., 2002).

In the present work we mapped, in a large group of subjects, the functional selectivity along three dimensions: object category preferences, motion sensitivity, and visual field eccentricity. The aim of the work was three-fold. First, we wanted to test the functional selectivity maps for common objects, whose recognition (as opposed to faces and words) does not necessarily rely

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*Correspondence: rafi.malach@weizmann.ac.il on high acuity. Second, given our finding of association between object preference and eccentricity within the VOT, we wanted to see whether this organization principle may also apply to the dorsal occipito-temporal cortex (DOT). Third, we wanted to search for organization principles that might unify the ventral and dorsal occipito-temporal cortex into more global entities.

It should be emphasized that our analysis was not intended to examine the issue of modularity versus distributed representation in high-order object cortex (Avidan et al., 2002; Haxby et al., 2001; Kanwisher, 2000). Thus, we used specific object categories simply as a mapping tool, since they provide robust, distinguishable, and replicable activations and since they are widely used by many research groups. Our analysis was confined to the nonretinotopic object-related activation found in the occipital and temporal lobes, moving from the ventral CoS to the dorsal transverse occipital sulcus (TOS), anterior to known retinotopic areas and posterior to area MT.

The present results reveal a consistent pattern of seven category-related regions within the occipito-temporal cortex. These include two foci of face-related activation, three foci of common object-related activation, and two foci of building-related activation. Although the size and exact locations varied across subjects, their spatial relationships were consistently preserved. Moreover, the same category-related transition from buildings to objects to faces was found both in the ventral occipito-temporal (VOT) cortex and dorsal occipito-temporal (DOT) cortex, so that the two subdivisions were arranged in a large-scale dorso-ventral *mirror-symmetry* structure, centered on the middle object-related region. In addition, similar to the center-periphery organization found in the VOT cortex, it appears that the DOT cortex was also organized by a similar principle. Thus, the entire set of object-related occipito-temporal regions could be placed, with minor distortions, into a single unified map of center-periphery organization. This global organization may hint at the possible route by which human object cortex might have differentiated into its specialized category-related subdivisions.

Results

Category-Related Parcellation of the Occipito-Temporal Cortex

Following the extensive research into the parcellation of occipito-temporal cortex using specific object categories, we searched, in 18 subjects, for consistent activation patterns related to the most commonly used categories: faces, buildings, and common object images. To delineate high-order object-related regions relative to low-level visual areas, we also included geometric patterns in the experiment. Each category was contrasted with the two other categories (e.g., faces versus buildings and objects). The average activation maps ($n = 18$, general-linear model with random-effect analysis) for these categories are shown in Figure 1. To appreciate the consistency of the pattern as well as the intersubject variability, we present in Figure 2 ten unfolded hemispheres from five subjects. The major foci of activation adjoining early retinotopic cortex (retinotopic borders indicated by black dotted lines) are indicated by small white arrows. Talairach coordinates of each of the category-related activation foci are shown in Table 1.

Previously (Grill-Spector et al., 1998a), we have divided the object-related LOC into two main subdivisions: a ventral one, termed the posterior fusiform gyrus (pFs), and a more dorsal one, in the vicinity of the lateral occipital cortex (LO; for review see Grill-Spector et al., 2001). Here we will present the results within a framework of two larger tentative subdivisions: (1) a ventral one, which we will refer to as ventral occipito-temporal (VOT) cortex, which extends from the pFs laterally to the CoS medially (approximate borders of the VOT are marked by the dashed rectangle in the left hemisphere in Figure 1); and (2) a dorsal partition, which we will refer to as dorsal occipito-temporal (DOT) cortex, which extends dorsally to the TOS and ventrally to the inferior temporal sulcus (ITS) (approximate borders of the DOT are marked by the dashed rectangle in the left hemisphere in Figure 1). Thus, taken together, the VOT and DOT encompass the entire band of higher-order object-related regions, adjacent and anterior to known retinotopic areas, from the CoS to the TOS (not including the parietal cortex and regions dorsal and anterior to MT).

Inspecting these two major partitions, we found the following three category-related subdivisions. (1) Face-related foci: two foci were identified (red regions in Figures 1 and 2), one in VOT overlapping the pFs (corresponding to the FFA), and one in DOT overlapping the inferior occipital gyrus (IOG) (corresponding to the OFA). In 14 out of 18 subjects, we also found a third focus anteriorly and dorsally to area MT/V5, and in 8 out of 18 subjects an additional face-related focus in the superior temporal sulcus (STS) (see Figure 1, right hemisphere). These anterior regions are known to be sensitive to eye movements and direction of gaze (Hoffman and Haxby, 2000; Puce et al., 1998) but were only weakly activated in the present study, probably due to the use of line drawings of faces or due to the reduced signal in anterior regions when using a surface coil (see Experimental Procedures). (2) Building-related foci: two major foci were identified (green regions in Figures 1 and 2), a ventral region overlapping the CoS (corresponding approximately to the PPA), and a dorsal one overlapping the TOS. (3) Object-related foci: three consistent regions were found (blue regions in Figures 1 and 2). These included a region in VOT, "sandwiched" between the face- and building-related activations, overlapping the medial bank of the pFs; a region at the ventral-anterior border of DOT, overlapping the ITS; and a third region located dorsally to the face-related activation of the DOT, overlapping the lateral occipital sulcus (LOS). An additional object-related region, which will not be discussed in the present study, was observed in the intraparietal sulcus (IPS).

Detailed Topographic Relationship between Object-Selective Activations

As can be seen from Figure 2, there were substantial variations in the size, distance, and absolute location of each object-related region. However, close inspection of Figures 1 and 2 reveals that the overall spatial arrangement was consistent. First, in the dorsal occipito-

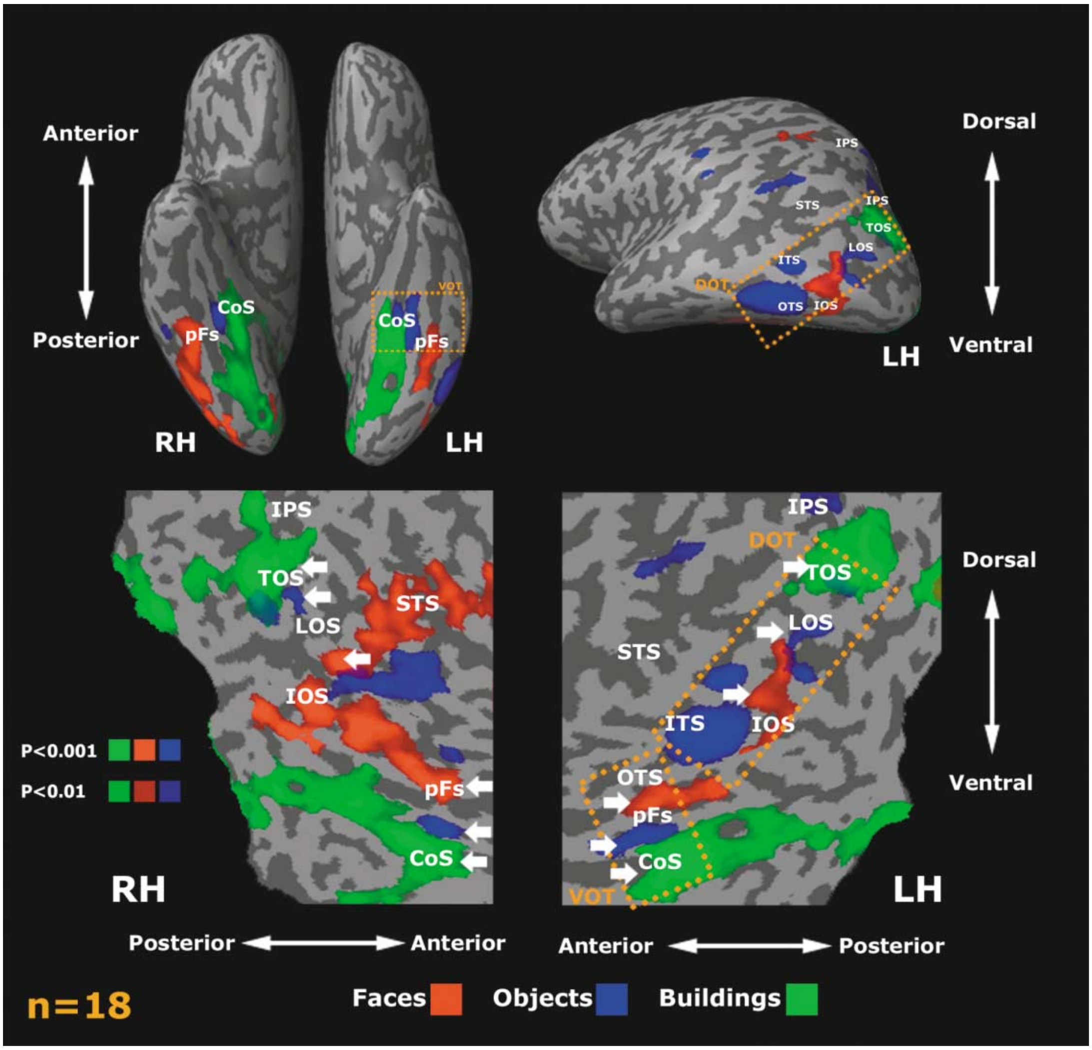

Figure 1. Mapping Activation to Faces, Buildings, and Objects

Averaged activation map (18 subjects, general linear model with random effect) for faces (red), objects (blue), and buildings (green), shown on a ventral (top left) and lateral (top right) view of inflated hemispheres and on unfolded hemispheres (bottom). Dashed rectangles in the left hemisphere denote the approximate location of the DOT and VOT partitions. Each category was contrasted with the two other categories (e.g., faces versus buildings and objects).

temporal (DOT) cortex, the category-related activation patterns were found to be arranged dorso-ventrally, starting with building-related activations most dorsally along the TOS, followed by object-related activity, which was followed by face-related activation (see white arrows in Figures 1 and 2). The same consistent spatial relationship appears also in the VOT going medial to lateral: the extensively documented building-related activation located medially along the CoS, followed by object-related activity in the medial bank of the pFs, followed by face-related activation located laterally along the pFs. An additional object-related region was located in the ITS between the dorsal and ventral subdivisions. Finally, in 6 out of 18 subjects, we also found an additional, more lateral object-related focus, along the occipito-temporal sulcus (OTS) (e.g., see right hemisphere in Figure 1 and subject EQ right hemisphere in Figure 2), which appears as an extension of the most ventral object-related focus found in the DOT.

An intriguing finding related to these maps was that the sequence of category-related activations in the DOT and VOT were arranged in a *mirror-symmetric* fashion relative to each other, centered around the object-related activation in the ITS. Thus, the dorso-ventral arrangement of buildings (B), objects (O), and faces (F) in the DOT was mirror symmetric to the same sequence along the medial-lateral arrangement in the VOT (see also top inserts in Figure 4).

This large-scale mirror-symmetry structure (B-O-F-O-F-O-B) was found in 15 out of 18 right hemispheres and in 11 out of 18 left hemispheres. In the remaining 10 hemispheres, at least one of the category-related regions was absent (see also Table 2), but no reversal of the spatial relationship between any given two regions was observed. Such consistent activation could not have emerged from randomly generated selectivity. The probability of finding a certain pattern in one subject due to random variability is 1/210 (7!/(2!·2!·3!) possible

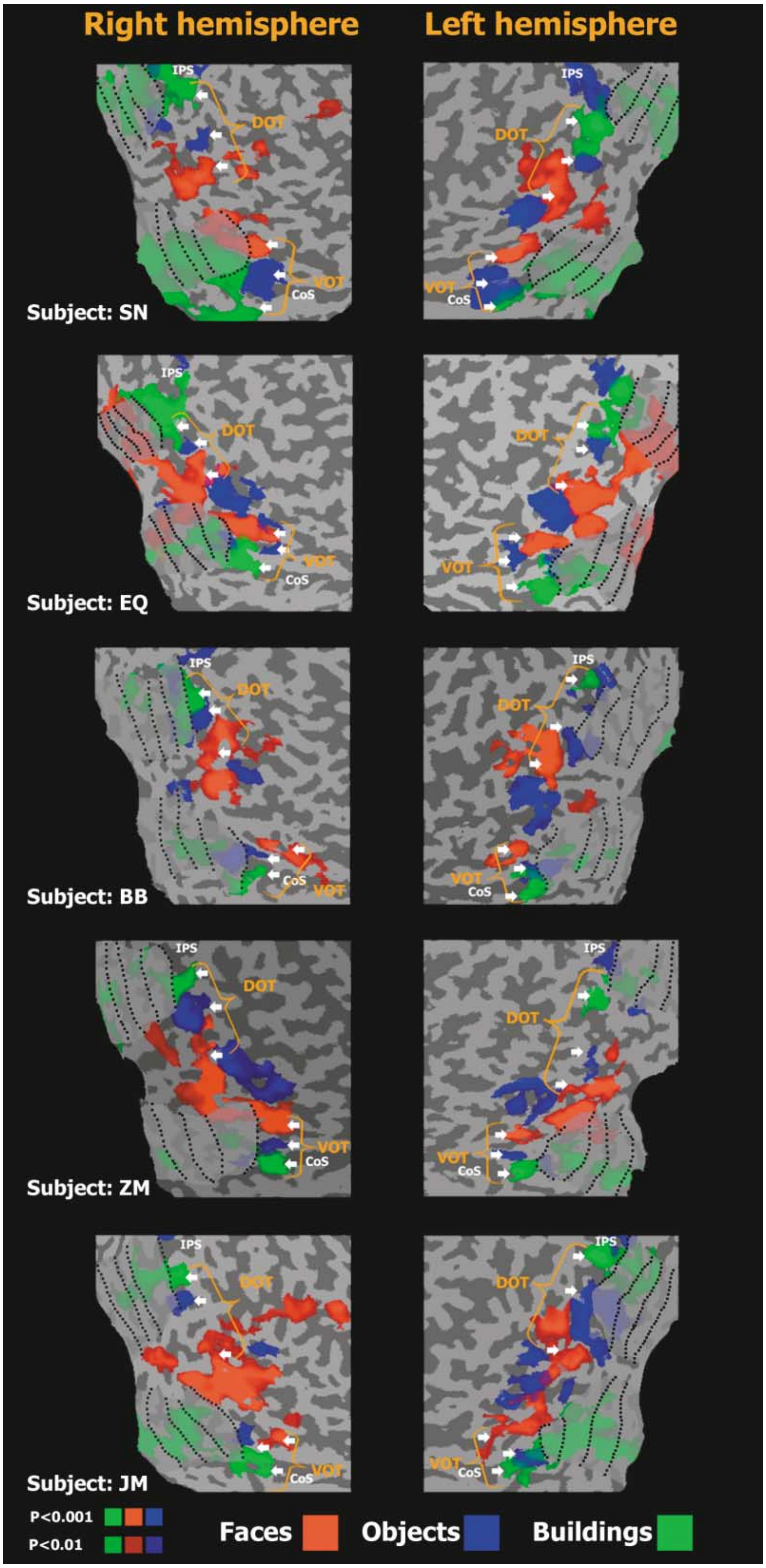

Figure 2. Category-Related Activation and Retinotopic Borders

Preferential activation for faces (red), objects (blue), and buildings (green) are shown on the unfolded right and left hemispheres of five different subjects. Black dotted lines denote borders of retinotopic visual areas V1, V2, V3, VP, V3A, and V4/V8. Orange brackets mark the face-, object-, and building-related activations in the VOT and DOT cortex (see also white arrow for each of the category-related regions). Note that starting from the medial ventral part of the VOT cortex and from the medial dorsal part of the DOT cortex, the activation shifts from buildings to objects to faces.

arrangements). Therefore, the probability of finding this pattern in 11 or 15 out of 18 hemispheres is extremely low (right hemisphere, $p < 10^{-31}$; left hemisphere, $p < 10^{-21}$, Binomial test).

Relationship to Early Retinotopic Cortex and Visual Field Meridians

Comparing the object-related activity patterns to retinotopic visual areas in 12 out of the 18 subjects (identified

Table 1. Talairach Coordinates

	Left Hemisphere				Right Hemisphere			
	n	X	Y	Z	n	X	Y	Z
VOT								
Faces (lateral pFs)	18	−38 ± 3	−48 ± 12	−19 ± 4	17	37 ± 4	−44 ± 10	−17 ± 4
Objects (medial pFs)	18	−30 ± 5	−42 ± 8	−17 ± 3	17	27 ± 4	−41 ± 10	−16 ± 3
Buildings (CoS)	18	−22 ± 2	−43 ± 6	−9 ± 2	17	24 ± 2	−40 ± 7	−10 ± 3
DOT								
Objects (ITS)	16	−44 ± 3	−61 ± 6	−7 ± 5	15	43 ± 3	−58 ± 7	−6 ± 4
Faces (IOG)	13	−42 ± 6	−74 ± 6	−8 ± 2	15	42 ± 4	−69 ± 9	−5 ± 8
Objects (LOS)	12	−39 ± 3	−79 ± 5	2 ± 6	13	37 ± 5	−75 ± 6	4 ± 5
Buildings (TOS)	14	−34 ± 4	−79 ± 4	12 ± 3	17	33 ± 4	−77 ± 3	12 ± 6
Other Areas								
Objects (OTS)	4	−41 ± 2	−46 ± 14	−10 ± 7	5	42 ± 4	−47 ± 8	−11 ± 5
Faces (MTG)	5	−43 ± 5	−69 ± 11	13 ± 6	13	45 ± 4	−51 ± 27	−3 ± 11
Faces (STS)	6	−51 ± 5	−48 ± 9	8 ± 3	6	52 ± 4	−41 ± 4	10 ± 4

Average Talairach coordinates of category related regions in the VOT, DOT, and more anterior category-related regions, as measured in the first experiment. Numbers are in mm ± SD.

through visual field meridian mapping; see Experimental Procedures) showed that these regions were located anterior to known retinotopic areas and posterior to area MT/V5. This is illustrated in Figure 2, where the object-related activations were mapped relative to the retinotopic borders (black dotted lines).

Note that the object-related activation seems to extend into early visual areas (in particular for buildings). This could be due to unbalanced distribution of low-level visual features between the different categories (e.g., higher spectral energy in the periphery for the building stimuli). To control for this possibility, we manipulated the size of face and building images (see Feature Distribution Experiment below). Also note that we did not find any statistical differences in the reaction time for each category in the one-back task (faces, 489 ± 73 SD; houses, 505 ± 71; objects, 490 ± 67; patterns, 504 ± 66; ANOVA, single factor $p < 0.93$, $F = 0.13$), nor in the correct responses (faces, 98.6; houses, 98.2; objects, 99.2; patterns, 98.6; ANOVA, single factor $p < 0.7$, $F = 0.45$). Thus, the activation of early visual areas could not be attributed to differences in the allocation of attentional resources to different categories during the one-back task.

Relationship to Major Cortical Sulci and Gyri

An important issue in mapping high-order visual areas is the extent to which any given functional preference is related to a specific sulcal and gyral pattern of the cortex (Fischl et al., 1999). When comparing the activation patterns across subjects, it became evident that different category-related activations were consistently associated with specific sulci. Such a relationship is useful since it can provide a straightforward reference system for the different functionally identified regions. To further examine the consistency of the relationship between these regions and the sulcal patterns across subjects, we quantified the probability of finding an overlap between a particular category-related region and a specific sulcus/gyrus. In this analysis we first marked the sulci and gyri on the unfolded hemispheres of each subject (using Duvernoy and Bourgouin, 1999; Van Essen and Drury, 1997) and then assessed the anatomical

Table 2. Probability of Finding Category-Related Activation in a Given Sulcus or Gyrus

	VOT				DOT						No activation
	CoS	Medial pFs	Lateral pFs	OTS	ITS	IOG	IOS	MOG	LOS	TOS/IPS	
VOT											
Houses	97% (35)										3% (1)
Objects		97% (35)									3% (1)
Faces			86% (31)	11% (4)							3% (1)
DOT											
Objects				14% (5)	72% (26)						14% (5)
Faces						55% (20)	20% (7)	8% (3)			17% (6)
Objects								17% (6)	52% (19)	6% (2)	25% (9)
Houses									30% (11)	56% (20)	14% (5)

The percentages of hemispheres (out of 36) showing activation to a specific object category in any given anatomical region. In parenthesis is the number of hemispheres.

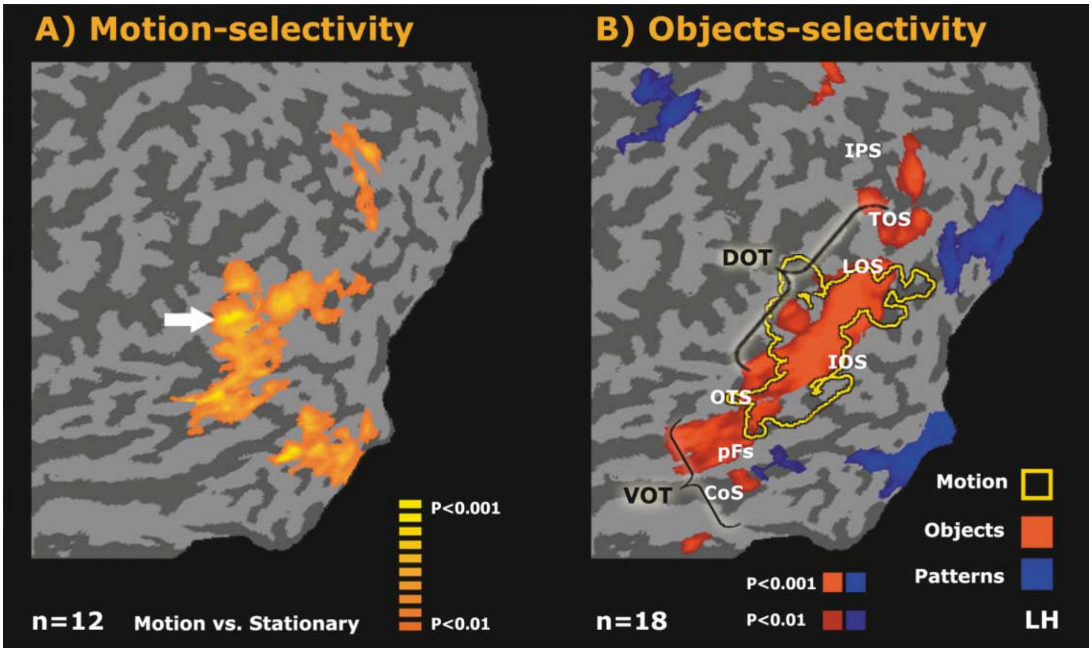

Figure 3. Motion Preference

(A) Averaged map ($n = 12$, general-linear model with random effect) for preferential activation to moving versus stationary circular gratings. White arrow denotes estimated location of MT/V5.

(B) The same motion-related activation (yellow contours) is superimposed on an average map (18 subjects) of preferential activation to objects (red) versus preferential activation to patterns (blue). Note that the motion-related activation overlaps with parts of the DOT but does not extend into the VOT region.

locations of the peak of activations for all seven category-related regions in each subject.

Table 2 summarizes this analysis. It can be seen that a very high consistency level was found in the VOT between the functional foci and the sulcal pattern (between 86% and 97% of hemispheres exhibited constant association between a specific sulcus or gyrus and a category-related activation). In the DOT, this relationship was somewhat less robust, particularly for the building-related region, which shifted between the TOS (56%) and LOS (30%). As for faces, in most of the cases (55%) the activation was in the IOG, but in a number of cases, face-related activation was shifted to the inferior occipital sulcus (IOS) (20%) and middle occipital gyrus (MOG) (8%).

Motion Sensitivity in the DOT

Since each object category produced preferential activation in both DOT and VOT, a question of interest was whether some functional tests might differentiate between these ventral and dorsal activations. Of the various functional tests examined, a particularly consistent differentiation was found to be associated with motion sensitivity. This result is shown in Figure 3. Figure 3A shows regions exhibiting motion preference, i.e., sensitivity to low-contrast moving versus stationary gratings. Typically, the area showing the strongest activation level ($n = 12$, $p < 0.0004$) to this contrast was area MT/V5 (Tootell et al., 1995; see white arrow in Figure 3A). However, lowering the statistical threshold sufficiently ($p < 0.05$) revealed additional motion-related regions both posterior and ventral to MT. Superimposing the boundaries of these motion-biased regions on the map of objects versus patterns (shown in red and blue, respectively, in Figure 3B) revealed that the motion bias was associated with the DOT and did not extend to the VOT region. Thus, motion sensitivity appears to be one of the characteristics distinguishing the VOT from most of the DOT. Note, however, that within the DOT the most dorsal occipito-temporal activation associated with the TOS (showing building-related activation in Figures 1 and 2) was not activated by the motion stimuli used in this study.

Eccentricity Maps in Occipito-Temporal Cortex

We have previously shown that the VOT cortex contains a center/periphery map extending from a periphery-biased representation in the CoS to a center-biased representation in the pFs (Levy et al., 2001). Here we mapped the eccentricity organization across the entire extent of human occipito-temporal cortex in 12 out of the 18 subjects (see Experimental Procedures for details). The results for a group analysis ($n = 12$, general linear model with random effect) compared to the category-related activation (Figure 4A, same maps as presented in Figure 1) are shown in Figure 4B. To examine the results quantitatively, we analyzed the relative activations to the center, mid, and peripheral visual field stimuli in each of the category-related foci. Each ROI was independently defined for each subject by its object preference (e.g., building-related activation in the CoS); we then used this unbiased ROI definition to derive the MR signal intensity in the eccentricity experiment. The results of this analysis for a group of 12 subjects are shown in Figure 4C. In addition, we calculated an eccentricity-bias index, which measured the relative contributions of center versus peripheral activations to the activity in these regions (Figure 4C, right panel; see Experimental Procedures).

As can be seen, in the activation maps (Figure 4B), in the time course analysis, and particularly in the eccentricity-bias index graph (Figure 4C), there was a gradual transition in the DOT from centrally biased face-related foci (yellow-red in the IOG; center versus periphery, two-tail paired T-test, $n = 12$, $p < 0.005$), through the more eccentricity-balanced common object-related regions (blue in the LOS, $p < 0.22$), and finally to peripherally biased building-related regions (green, in the TOS, $p < 0.005$). A similar transition from centrally biased face-related foci (yellow-red in the lateral pFs, $p < 0.005$), through a more eccentricity-balanced common object-related transition zone (blue in the medial pFs, $p < 0.03$), to a periphery-biased building-related region (green in the CoS, $p < 0.005$) could be observed also in the VOT.

Note that the object-related region in the ITS (adjoining the pFs dorsally) showed a slight center-bias preference (not shown), which distinguishes this region from the other two object-related regions (medial pFs and LOS), which showed less eccentricity preference. Note also that we did not find a preferential activation to the mid stimuli over the center and periphery stimuli in any of the activation foci (Figure 4C). This is in line with previous observations of a shrunk mid-periphery representation in high-order object areas (Levy et al., 2001; Tootell and Hadjikhani, 2001).

Finally, the eccentricity map in the DOT was arranged in a mirror symmetry to the map in VOT (compare the direction of arrows in DOT and VOT in the central insets of Figures 4A and 4B). Together, the eccentricity maps in the DOT and VOT formed a single eccentricity organization, centered on the foveal representation in the ITS and pFs, which was remarkably continuous with the eccentricity map of early visual cortex.

Features or Categories?

In many of the subjects, the apparent object-related activation seemed to extend into low-order retinotopic cortex (e.g., Figure 2). Such a spread might be attributed either to an unequal center/periphery distribution of low-level visual features of the different categories or to feedback activation from high-order object-related regions. To distinguish between these two alternatives, we compared the activation pattern to regular faces and buildings (Figure 5A) with the activation pattern to larger faces and smaller buildings (Figure 5B). The white dotted line indicates the estimated anterior border of retinotopic areas. Similar design was used by Levy et al. (2001) to rule out the possibility that unbalanced feature distribution governs the eccentricity bias found in the VOT; here we applied the same design for the DOT.

Comparing the two figures, it is clear that in high-order occipito-temporal cortex (anterior to the white dotted line), the activation pattern was less sensitive to changes in the object size, at least for the specific parameters used in the experiment (regular faces versus regular buildings or large faces versus small buildings; see Experimental Procedures for details). Thus, face images (red) consistently activated center-biased regions (in the IOG and pFs), while buildings activated periphery-biased regions (in the CoS and TOS) regardless of image size (regular, Figure 5A; large or small, Figure 5B). In contrast, at the most posterior regions, corresponding to early retinotopic areas, activation was determined mostly by size changes, regardless of the object category. Thus, large faces activated, as expected, a more peripheral representation (red arrows in Figure 5B) compared to small buildings (green arrow).

Finally, it seems that there was a gradual transition from low-level visual regions whose response was determined primarily by retinotopy, to high-order object areas whose response was determined primarily by the category preferences (at least up to the size change used in this experiment). Those intermediate regions appeared to overlap with intermediate retinotopic areas such as V4/V8 ventrally and V3A dorsally. Note, however, that in addition to the strong category dependency, anterior object areas also exhibited consistent eccentricity biases, provided that the object shapes were kept identical while the visual field eccentricity was manipulated (see Hasson et al., 2002).

Discussion

The main result of the present study is the finding of an object-based mirror-symmetric organization in human occipito-temporal cortex (Figure 4A). This finding is intriguing since it extends the principle of mirror-symmetric organization, which is the hallmark of early retinotopic cortex (Baizer et al., 1991; Boussaoud et al., 1991; Gattass et al., 1997) and even of topographic maps in other sensory modalities (Kaas and Collins, 2001) to high-order human object cortex. The two symmetric divisions of this mirror organization are (1) the dorsal-occipito temporal (DOT) cortex, which contains a sequence of category-related activations moving from building-related (TOS) to object-related (LOS) to face-related (IOG) regions, and (2) the ventral occipito-temporal (VOT) cortex, moving in the opposite direction from building-related (CoS) to object-related (medial pFs) to face-related (lateral pFs) regions. Moreover, the entire set of object areas within the occipito-temporal cortex could be placed, with minor distortions, within a single unified center-periphery map (Figure 4C, see also Figure 7). This large-scale organization points to the possible development of high-order visual areas, through extension and specialization of a single proto-representation.

Nomenclature

In this study we suggest to divide the entire band of occipito-temporal object-related regions (see activation for objects versus patterns [red] in Figure 3B) into two main tentative partitions: VOT and DOT. This subdivision is supported by the finding of a full eccentricity organization in each of the regions (Figure 4C).

How is this subdivision related to the lateral-occipital complex (LOC), defined by preferential activation to object images (including faces) compared to textures and scrambled-object images (Malach et al., 1995)? The LOC was divided into two entities, LO dorsally and pFs ventrally (Grill-Spector et al., 1998a). Considered within the

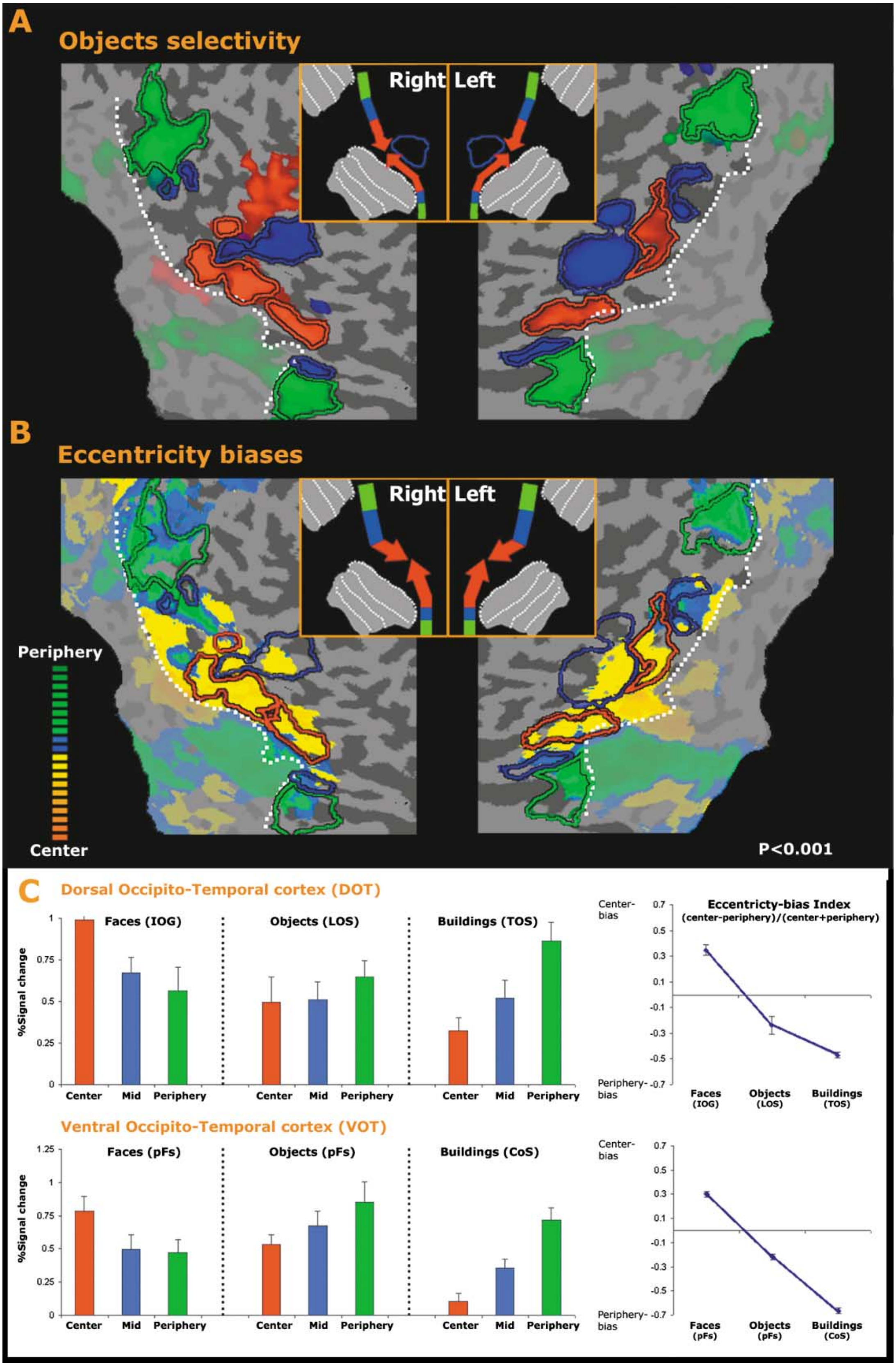

Figure 4. Relationship between the Category-Related Map and the Eccentricity Map

(A) Averaged activation map (n = 18, left and right hemispheres, same map as in Figure 1) showing preferential activation for faces (red), objects (blue), and buildings (green).

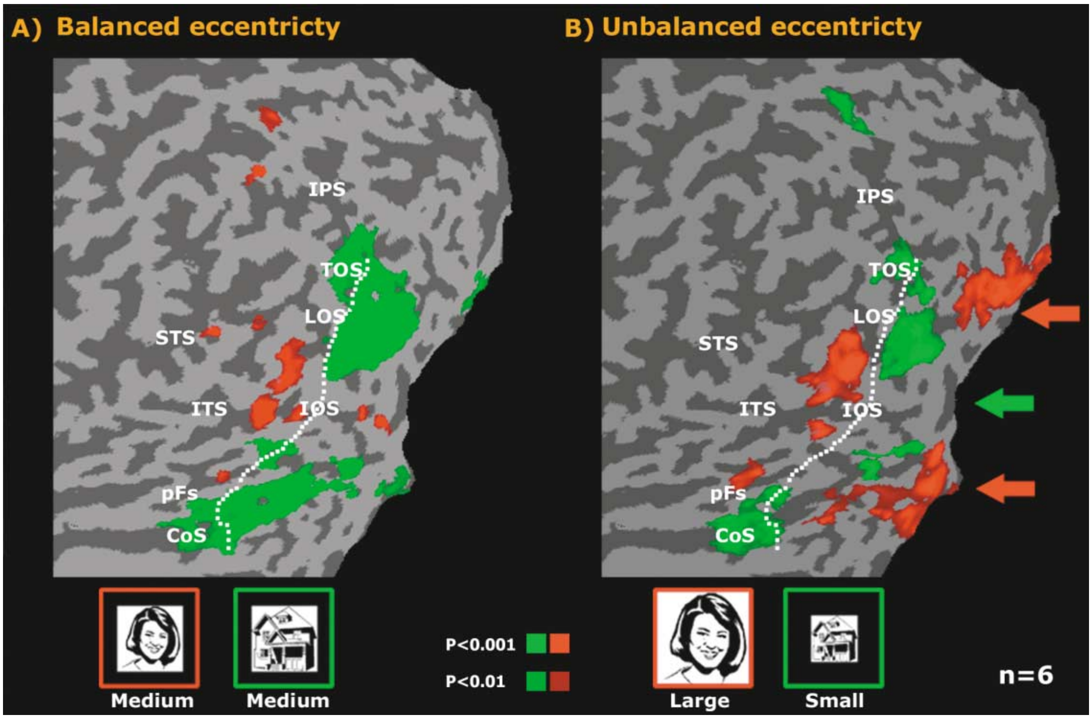

Figure 5. Feature Distribution Experiment

(A) Averaged map (six subjects; general-linear model with random effect) for preferential activation to face images (red) and building images (green). Images were of the same size as in the first experiment (12° × 12°). Dotted line indicates the estimated anterior border of retinotopic areas.

(B) Preferential activation to large faces (17.5° × 17.5°, red) compared to small buildings (5.8° × 5.8°, green). Note that in higher-order object areas, the activation for faces was always (in A and B) "sandwiched" between two building-related regions (CoS and TOS), regardless of the image size. In contrast, the activation in early retinotopic areas was affected by the image size, where small buildings activated center-bias regions (green arrow), while large faces activated periphery-biased regions (red arrows).

context of the present results, LO includes the central and mid-peripheral representations of the DOT, while the pFs include the center and mid-periphery of the VOT. Thus, the LOC overlaps the face- and object-related activation, excluding the building-related activation in the CoS (corresponding to the PPA) and the more dorsally located building-related activation in the TOS. For the purposes of defining activation to common objects and faces, the LOC, LO, and pFs definitions are perfectly valid and can be used as such. The VOT and DOT extend the parcellation of the LOC by incorporating the periphery-bias representation in the CoS and in the TOS and the large-scale mirror-symmetry structure.

The present study identified between seven and ten object-related regions within the occipito-temporal cortex. When referring to such definitions, we adopted the naming conventions of Kanwisher and colleagues, i.e., to refer to the main object category preference in conjunction with the main anatomical landmark. However, it should be emphasized that these names are tentative, since a more distinct functional characteristic might emerge in future studies. In addition, since the level of modularity of these entities is still debated, we prefer to refer to the activations as "regions" rather than the more definitive term "areas."

Relation to Other Studies

In this study we used three distinct categories (faces, buildings, and common objects) to map category-related activation patterns in high-order object areas. However, other studies reported additional category-related activation patterns, such as specific activations for chairs (Ishai et al., 1999), tools (Beauchamp et al.; Chao et al., 1999; Hasson et al., 2002), cars (Halgren et

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(B) Averaged activation map showing the transition from periphery-biased regions (green-blue) to center-biased regions (red-yellow) in the DOT and VOT (n = 12, general-linear model with random effect). The face-, object-, and building-related activations (red, blue, and green contours, respectively) are superimposed on the eccentricity map. Insets in the center illustrate the *mirror-symmetric* arrangement that was evident both in the object-related map (inset in A) and in the eccentricity-bias map (inset in B). Note the gradual transition from periphery-biased regions (green), through a more eccentricity-balanced region (blue) to center-biased regions (yellow-red), both in the DOT and VOT.

(C) The mean percent signal change (n = 12) for center (red bars), mid (blue), and periphery (green) conditions in the face- (IOG), object- (LOS), and building- (TOS) related regions in the DOT and the face- (pFs), object- (medial pFs), and building- (CoS) related regions in the VOT. Signal change was obtained from voxels that showed preferential category-related activation in the first localizer experiment ("external localizer"). Right: eccentricity-bias index plotted for each region. Positive values indicate a center bias, and negative values indicate a periphery bias. Note the gradual change from center-bias regions to periphery-bias regions both in the VOT and the DOT.

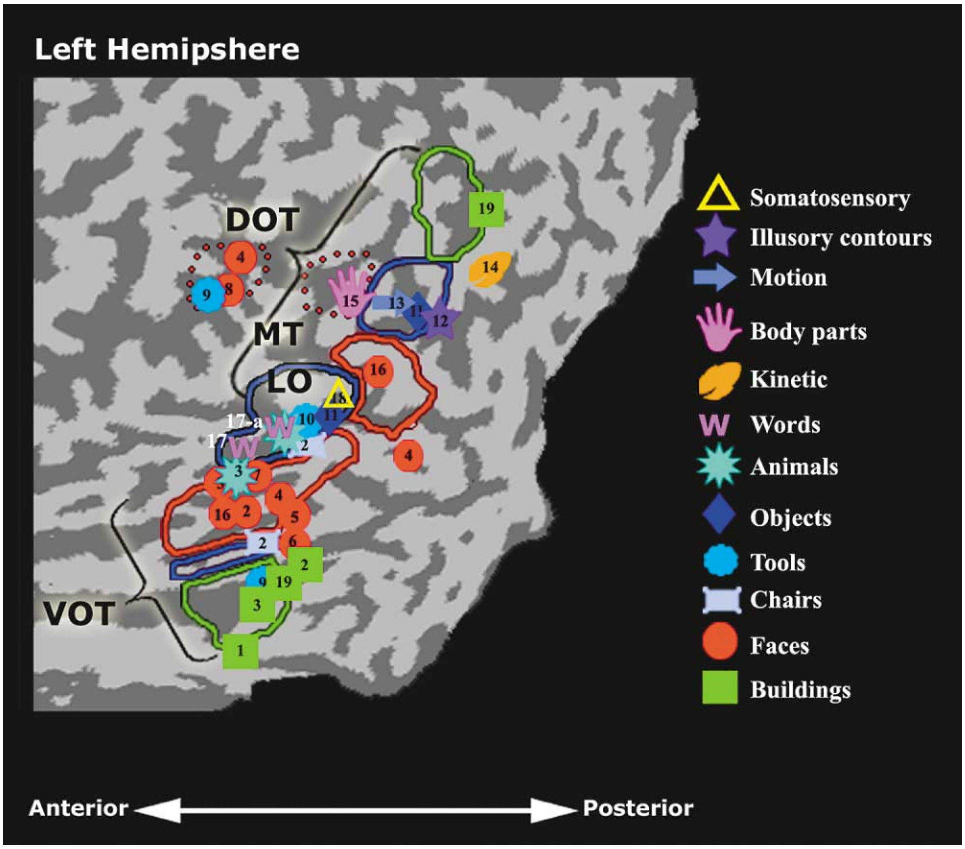

Figure 6. Category-Related Activation in Other Relevant Studies

Summary of category-related activation to the following object categories: buildings, faces, tools, chairs, animals, common objects, kinetic movement, body parts, motion objects, illusory contours, words, and somatosensory objects, obtained from Talairach coordinates reported in 18 different studies. The numbers appearing on the category icons represent the study number as listed: 1, Epstein and Kanwisher, 1998; 2, Ishai et al., 1999; 3, Maguire et al., 2001; 4, Hoffman and Haxby, 2000; 5, George et al., 1999; 6, Kanwisher et al., 1997; 7, Halgren et al., 1999; 8, Puce et al., 1998; 9, Chao et al., 1999; 10, Beauchamp et al., 2002; 11, Grill-Spector et al., 1999; 12, Mendola et al., 1999; 13, Kourtzi et al., 2002; 14, Van Oostende et al., 1997; 15, Downing et al., 2001; 16, Puce et al., 1996; 17, Hasson et al., 2002; 18, Amedi et al., 2001; 19, Haxby et al., 1999. The body parts-related region (15) is estimated based on MNI coordinate system. The word-related activation (^{17A}W) is based on average activation from six different studies as reported in Hasson et al. (2002). Note the substantial consistency of the various object-related activations across the different studies.

al., 1999), animals (Chao et al., 1999; Maguire et al., 2001), words and letter strings (Fiez and Petersen, 1998; Hasson et al., 2002; Puce et al., 1996), and recently also for body parts (Downing et al., 2001). How do these findings relate to our functional subdivision? Figure 6 summarizes the results from 18 studies that reported the Talairach coordinates of category-related activation.

First, the three main categories used in this study (see colored contours) activated similar anatomical locations in other studies as well. Thus, faces activated two regions, one in the pFs (George et al., 1999; Halgren et al., 1999; Hoffman and Haxby, 2000; Ishai et al., 1999; Kanwisher et al., 1997; Maguire et al., 2001; Puce et al., 1996) and one in the vicinity of the IOG (Hoffman and Haxby, 2000; Puce et al., 1996), whereas buildings activated the CoS (Epstein and Kanwisher, 1998; Ishai et al., 1999; Maguire et al., 2001) and the TOS (Haxby et al., 1999), and objects and tools activated the ITS (Beauchamp et al., 2002; Grill-Spector et al., 1999) and LOS regions (Grill-Spector et al., 1999).

Second, at a finer scale it seemed that additional categories also significantly activated, albeit to a lesser extent, each of these regions. Thus, tools activated the building-related CoS (Chao et al., 1999; see also activation for cars in Halgren et al. [1999]), animals activated the face-related pFs (Maguire et al., 2001; Tong et al., 2000), chairs (Ishai et al., 1999) activated the object-related regions in the ITS and pFs; and words and letters (Fiez and Petersen, 1998; Hasson et al., 2002; Puce et al., 1996) activated the object-related region in the OTS/ITS, with a strong left hemisphere lateralization. This more distributed aspect of the activations was indeed emphasized and discussed in recent reports (Avidan et al., 2002; Haxby et al., 2001).

Third, objects defined by motion or stereo-dots (Grill-Spector et al., 1999; Kourtzi et al., 2002; see also Gilaie-Dotan et al., 2002) were reported to activate the object-related LOS region. These results are consistent with the motion sensitivity of this region found in the present study (see Figure 3). Note also that objects defined by illusory contours (Mendola et al., 1999) or by kinetic motion (Van Oostende et al., 1997) were reported to

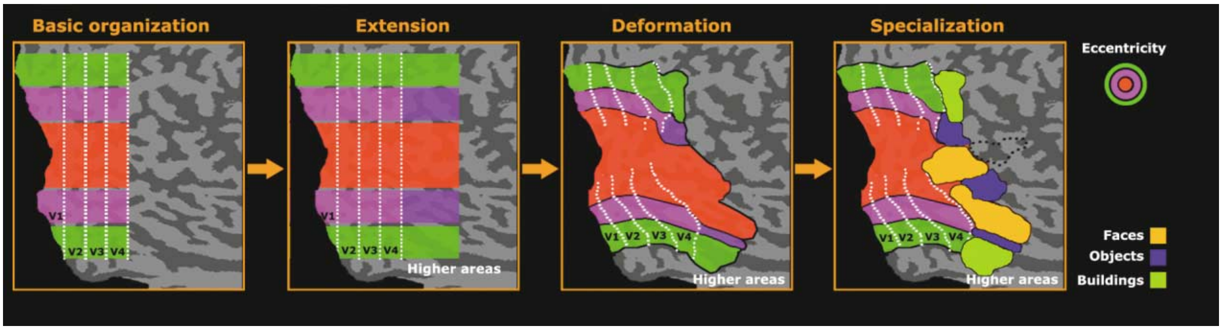

Figure 7. A Hypothetical Scheme for the Formation of High-Order Object Areas

A schematic proposal of three development stages in which a proto-map of center-periphery organization (Basic Organization) in early retinotopic areas (V1 to V4/V8, white dotted lines) is extended anteriorly into high-order object cortex (Extension), distorted ventrally along the cortical surface (Deformation), and finally undergoes local specialization (based, in part, on eccentricity-related acuity demands), leading to the observed pattern of different object-related activations (Specialization).

activate regions in the vicinity of the LOS. Finally, it is interesting to note that two additional object-related regions were found in the temporal lobe anterior to those regions: one dorsal and anterior to area MT that responds to body parts (Downing et al., 2001; see also activation for biological motion in Beauchamp et al., 2002), and one in the superior-temporal sulcus that responds to the direction of gaze (Hoffman and Haxby, 2000; Puce et al., 1998). It could be that these regions (see Figure 1, right hemisphere) are part of an additional object-related network specialized for analyzing different forms of biological motion.

Large-Scale Topography

From the previous discussion it may appear that occipito-temporal cortex is hopelessly complex, containing a bewildering diversity of subdivisions. Surprisingly, when the eccentricity-biased organization is taken into account, this highly complex organization is substantially simplified into a single, unified eccentricity map. Thus, from a broader perspective, the entirety of occipitotemporal cortex ranging from the TOS dorsally to the CoS ventrally can be described as an elongated central representation (Figure 4B, red-yellow patch) “sandwiched” between two peripheral representations (green patches). These central and peripheral representations are separated by transition zones in the LOS dorsally and medial pFs ventrally (blue patches).

This large-scale organization can be evident also within the organization of the category-related subdivisions. Here it is manifested in the dorso-ventral *mirror-symmetry* axis (Figure 4A). Thus, the sequence of buildings to objects to faces of the VOT duplicates itself in a mirror-symmetric fashion along the DOT (see insets in Figures 4A and 4B).

This remarkable organization raises the intriguing possibility that it may point to the process by which high-order human object areas emerged. Such a hypothetical sequence of events is depicted in Figure 7. Note that starting from a basic center-surround organization (Figure 7, Basic Organization), a simple three-stage process can account for our entire data set. In this process, the retinotopic eccentricity map is first extended anteriorly (Extension), then distorted ventrally (Deformation), and finally undergoes eccentricity-related specialization (Specialization) to different object category representations.

Such a scheme implies that in the development (in evolution or during the development of the organism) of the visual system, the retinal polar angle dimension is repeatedly duplicated, while the eccentricity dimension is maintained throughout all retinotopic areas and most of higher-order object-related regions. A somewhat analogous pattern has recently been demonstrated in rodent somato-sensory maps (Fukuchi-Shimogori and Grove, 2001). While this scheme is still hypothetical, it does illustrate that the complex organization of human object areas is likely to be a manifestation of a simpler, larger-scale organizing principle.

The Relationship between Category-Related Activation and Eccentricity

Our results confirm and extend our previous finding, in the VOT, of an association between faces and central visual field bias and between buildings and peripheral bias. Here we found a parallel association between object categories and eccentricity in the DOT, where buildings were associated with peripheral representations in the TOS and faces with central representations in the IOG (see Figure 4). The situation with objects was more complex. Two foci of object activations overlapped the eccentricity “transition” zones (Figure 4); however, a third, and highly robust, object-related focus was associated with a central visual field bias (ITS).

We have previously hypothesized that the association with visual field eccentricity might be related to the different acuity needs associated with different recognition processes (Malach et al., 2002). Thus, central representations having a higher magnification factor will be associated with visual processes requiring a fine detail analysis (e.g., detection of facial expression or reading words), while peripheral ones will be associated with visual processes requiring large-scale integration (such as navigation).

The present finding of an association between the common object-related activation and the intermediate “transition zone” eccentricities appears compatible with this hypothesis, with objects presumably requiring intermediate levels of magnification in between faces and buildings. Thus, objects are likely to activate a variety of recognition processes associated with a more balanced mix of different acuity demands.

Are the Activations in the DOT Truly Object Category-Related?

The main interest in our present results is the discovery of object-related mirror symmetry that places the DOT and VOT in a single, large-scale organization. It is easier to understand this organization if both the DOT and the VOT truly represent object-related activations; but it could be argued, and particularly for the DOT, that its preferential object category activations might be due to low- or middle-level visual features rather than more "holistic" object representations. However, previous studies strongly demonstrate that the activation in the DOT, or at least its central part, cannot be attributable to local image features. Clear demonstrations of the holistic nature of the representation in these regions was obtained by using the Rubin Vase-face illusion (Hasson et al., 2001), by the adaptation studies of Kourtzi et al. (Kourtzi and Kanwisher, 2001), and by the strong convergence of various visual cues in these regions shown by Grill-Spector (Grill-Spector et al., 1998a). All these results clearly point to the fact that the DOT selectivity is holistic in nature and cannot be attributable to low-level local features.

Another point that needs clarification concerns the absolute selectivity in these regions. Our results pertain only to *relative* activations when comparing different object categories. Thus, the finding of face-related activation in this study only implies a relatively higher activation to faces when compared to houses and common objects and should not be interpreted as indicating a higher activation to faces compared to all other potential object categories. However, the intriguing finding is that even when using relative activations, we find a consistent mirror-symmetry arrangement. Moreover, similar results were found for more specific common object categories such as tools (Hasson et al., 2002) and chairs (Ishai et al., 1999), which suggests that this organization principle is robust and does not rely on the specific stimuli used in this experiment.

Functional Distinctions between DOT and VOT

One puzzle that remains in the scheme proposed here is the functional differentiation between the dorsal and ventral occipito-temporal representations. Topographically, these two parts appear to be mirror-symmetric duplications of the eccentricity map. This raises the question of the functional distinction between these two subdivisions.

Previous studies have outlined several functional differences, at least between the dorsal and ventral parts of LOC. Thus, using the fMR adaptation approach, Grill-Spector et al. have shown that the dorsally located LO shows higher sensitivity to position and scale changes compared to the more ventrally located pFs (Grill-Spector et al., 1999). Beauchamp et al. and Kourtzi et al. have shown that DOT but not VOT are associated with object motion (Beauchamp et al., 2002; Kourtzi et al., 2002).

In the present study we identified two distinctions between the dorsal and ventral occipito-temporal cortex. First, object representations appeared to be much more widespread dorsally than ventrally (see blue regions in Figures 1 and 2). Second, with the exception of the building-related activation, dorsal regions showed a higher motion preference compared to ventral regions (Figure 3). Although the building-related TOS did not show such preference, this may be attributed to shape factors of the motion stimuli used in the motion experiment (e.g., the gratings frequency and size; see Experimental Procedures), which may have been too fine for the peripherally biased TOS.

In attempting to find a common principle, which may underlie all these distinctions between DOT and VOT, it appears that dorsal object regions are more involved with relations between objects and space (such as position, motion, and scale), while ventral regions are more associated with identity (see also Beauchamp et al., 2002). It should be noted that DOT is at close proximity to classical dorsal stream regions (Ungerleider and Mishkin, 1982), such as MT/V5+ and parietal cortex. It is thus tempting to speculate that between the functional differentiation of dorsal (space) and ventral (identity) streams, DOT might occupy an intermediate position dealing with the spatial aspects (e.g., movement, kinematics) of object recognition. However, more data are needed to confirm this conjecture.

Experimental Procedures

Subjects

Nineteen healthy subjects (10 women, ages 24–50) participated in one or more of the experiments. The same 12 subjects participated in four of the experiments, which included the object, eccentricity, motion, and meridian localizers. This substantial overlap of functional maps enabled us to search for large-scale topographical relationships within each subject. A subgroup of six subjects participated in the Feature-distribution experiment. All subjects had normal or corrected to normal vision and provided written informed consent. The Tel-Aviv Sourasky Medical Center approved the experimental protocol.

MRI Setup

Subjects were scanned in a 1.5T Signa Horizon LX 8.25 GE scanner equipped with a custom quadrature surface coil (Nova Medical Inc., Wakefield, MA) to provide a high signal-to-noise ratio in occipito-temporal brain regions. However, when using the surface coil, the signal drops, on average, by 15% when moving anteriorly to the middle temporal gyrus (MTG) compared to calcarine sulcus and by 25% in the STS. Blood oxygenation level-dependent (BOLD) contrast was obtained with gradient-echo echo-planar imaging (EPI) sequence (TR = 3000, TE = 55, flip angle = 90°, field of view 24×24 cm^2, matrix size 80×80). The scanned volume included 17 nearly axial slices of 4 mm thickness and 1 mm gap. T1-weighted high-resolution ($1 \times 1 \times 1$ mm) anatomical images and 3D-spoiled gradient echo sequence were acquired on each subject to allow accurate cortical segmentation, reconstruction, and volume-based statistical analysis.

Experiments

Face, Building, and Object Localizer Experiment

Eighteen subjects participated in this experiment. The visual stimuli used included line drawings of faces, buildings, common man-made objects, and geometric patterns. Nine images of the same type were presented in each epoch; each image was presented for 800 msec and was followed by a 200 msec blank screen. An interleaved short block design was used in the experiment. Each epoch lasted 9 s, followed by a 6 s blank screen. A central red fixation point was present throughout the experiment. Each experimental condition was repeated 7 times, in pseudo-random order. The experiment started with 27 s and ended with 9 s of a blank (fixation only) screen. The experiment lasted 450 s. During the experiment, one or two consecutive repetitions of the same image occurred in each epoch. Subject's task was to covertly report whether the presented stimulus was identical to the previous stimulus or not.

Motion Experiment

Twelve subjects participated in this experiment. The experiment lasted 420 s, visual stimuli were low-contrast rings (rectangular rings surrounding the central fixation point, 0.5 cycles/degree; duty cycle $= 0.2$; thin white rings on a thicker black background). In the present study the stimulus was presented at low luminance contrast (1.5%). Two different 18 s experimental conditions were used: a stationary condition, in which visual stimuli were presented every 3 s, and a moving condition in which the rings expanded for 2 s and contracted for 2 s. Subjects were instructed to fixate a fixation point throughout the experiment. For each subject area MT/V5 was defined by a correlation test contrasting the moving and stationary conditions. The setting was similar to the one used in Tootell et al. (1997).

Eccentricity Mapping Experiment

Twelve subjects participated in this experiment. The visual stimuli included line drawings of objects, which were located in three eccentricities of the visual field: center (a circle of 1.4° diameter), mid (a ring of 2.5° inner diameter and 5° outer diameter), and periphery (a ring of 10° inner diameter and 20° outer diameter). Pictures were presented in 18 s blocks, where each picture was shown for 250 ms. Subjects were requested to fixate a small fixation dot. Visual epochs alternated with 6 s blanks. Four cycles of the stimuli were shown. The experiment started with 24 s and ended with 12 s of a blank screen. The experiment lasted 414 s.

Meridian Mapping Experiment

Twelve subjects participated in this experiment. The representations of vertical and horizontal visual field meridians were mapped and used to delineate the borders of early retinotopic areas (DeYoe et al., 1996; Engel et al., 1994; Grill-Spector et al., 1998b, 2000; Sereno et al., 1995). Detailed description of the methods is provided in Grill-Spector et al. (1998a).

Feature-Distribution Experiment

Six subjects participated in this experiment. They were presented with pictures of faces and buildings as in the first experiment ($12° \times 12°$) and with two additional categories: large faces (same faces enlarged to a size of $17.5° \times 17.5°$) and small buildings (same buildings reduced to a size of $5.8° \times 5.8°$). Presentation procedure and task were the same as in the first experiment.

Data Analysis

fMRI data were analyzed with the "BrainVoyager" software package (Brain Innovation, Masstricht, Netherlands) and with complementary in-house software. The cortical surface in a Talairach coordinate system (Talairach and Tournoux, 1988) was reconstructed for each subject from the 3D-spoiled gradient echo scan. The obtained activation maps were superimposed on the unfolded cortex and the Talairach coordinates were determined for the center of each ROI (region of interest). Preprocessing of functional scans included 3D-motion correction and filtering out of low frequencies up to 10 cycles per experiment (slow drift). Spatial smoothing using Gaussian filter of 4 mm full width at half maximum value (FWHM) was applied to data from the first experiment.

General Linear Model

Statistical mapping was based on the General Linear Model (Friston et al., 1995). Our analysis consisted of a multiple regression with a regressor for each condition in the experiment, using a box-car shape and assuming a hemodynamic lag of 3 s. The analysis was performed independently for the time course of each individual voxel. After computing the coefficients for all regressors, we performed a T test between coefficients of different conditions (e.g., faces versus buildings and common objects; the coefficient of the face predictor was compared to the average of the building and common object predictors). To obtain the multisubject maps, time series of images of brain volumes for each subject were converted into Talairach space and z-normalized. The multisubject maps were obtained using a random effect procedure (Friston et al., 1999). The multisubject functional maps were projected on an inflated or unfolded Talairach normalized brain. Significance levels were calculated taking into account the minimum cluster size and the probability threshold of a false detection of any given cluster (Forman et al., 1995). This was accomplished by a Monte Carlo simulation (AlphaSim by B. Douglas Ward, a software module in Cox, 1996); using the combination of individual voxel probability thresholding and minimum cluster size of 10 voxels, the probability of a false positive detection per image was determined from the frequency count of cluster sizes within the entire cortical surface (not including white matter and sub nuclei). The minimum significance level, corrected for any given cluster, was $p < 0.01$. Color scales indicate the statistical level ranging from $p < 0.01$ (darker colors) up to at least $p < 0.001$ (brighter colors).

Two-Color Map

When mapping the relative contribution of two functional responses (Figure 4B, "center" versus "periphery") the color coding represents the relative contribution of either set. The exact color used depends on the level of differential contributions by each predictor set. Green represents a strong contribution of the periphery predictor over the center predictor, while red represents the opposite trend (i.e., center dominance). Shades of yellow and blue represent a more balanced eccentricity-bias. Multisubject maps were generated using random effect analysis.

Time Course Analysis

To obtain an unbiased statistical test, we used the external localizer approach. In this procedure we used the face, building, and object localizer experiment to localize the seven different category-related regions in each subject. We then used these ROIs to evaluate the activation level in the eccentricity experiment. Thus, the measured activity in the eccentricity experiment was unbiased by the statistical test used to define each ROI.

Eccentricity-Bias Index

An eccentricity-bias index was calculated for each category-related region. For each defined region we measured the relative eccentricity preference by subtracting the center-bias activation (% signal change) from the periphery-bias activation and dividing them by the sum:

$$(\text{center} - \text{periphery})/(\text{center} + \text{periphery}).$$

Thus, the eccentricity-bias index ranges between 1 and -1, positive values indicating a center-bias, and negative values indicating a periphery-bias.

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