Mapping of shape-related areas in the human visual cortex using fMRI

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Abstract

The human occipito-temporal cortex has been implicated in object recognition in a number of neuroimaging studies. These studies revealed a rich and complex specialization pattern within this cortical area, in which different regions are preferentially activated by certain object categories compared to others. The main examples are a region showing relatively enhanced activation to face images and a cortical region sensitive to images of buildings and scenes. These specializations clearly reflect a robust phenomenon, since the neuroanatomical relationships between the functionally specialized regions are highly consistent across subjects and studies. Thus, the activation to face images is always located in the vicinity of the fusiform gyrus (pFs), laterally to the activation to building images, which lies in the vicinity of the collateral sulcus (CoS).

The principles underlying the category-related activation are not yet clear, and may include shape factors, task-related factors and visual expertise effects. However, none of these factors explains the consistent anatomical relationships between different categories. In addition, it should be noted that the activation to a certain category is relative rather than absolute; each specialized region shows substantial activation to other object categories as well, which might hint at a more distributed nature of object representations.

In the first part of my thesis we found a unifying principle that could explain the anatomically consistent category-related specializations. In the second and third parts we explored the characteristics of the building and face related regions within this global organization. Finally, in the fourth part we examined the representation of a single object within the object-related areas and assessed the number of neurons participating in such a representation.
Early visual areas are retinotopically organized, such that each area contains an orderly map of the visual field, whose origin is the center of the visual field and whose axes are the polar angle and the distance from the center, or the eccentricity. The eccentricity dimension is a robust organizational principle which unites all the early visual areas into one entity. Given the proximity of object-related visual areas to early ones we hypothesized that the eccentricity organization might extend into high-order object areas. Using images of objects shown in three different eccentricities we found that most of the occipito-temporal cortex was organized in a center-periphery organization, and that consistent relationships existed between certain object categories and certain eccentricity preferences. Specifically, face-related regions were associated with central visual field representations whereas building-related regions were related to peripheral ones. Our interpretation of the results is that object-related regions are organized according to resolution needs, with objects whose identification relies on fine details, such as faces, activating central regions and objects whose recognition entails large scale integration, such as buildings, activating peripheral regions.

In the second study we explored the source of the peripheral bias found in building-related regions. First, in the previous study the peripheral bias was obtained when activation, elicited by a number of enlarged objects shown in a peripheral annulus, was compared to that elicited by a single central small object. Therefore, the peripheral effect might be due to the peripheral location of the stimuli, to the large area they covered or to multiplicity of objects shown in the periphery. Second, there could be an interaction between the category-related organization and the eccentricity bias; i.e. it could be that the periphery effect is stronger for certain object categories compared to others. We showed that the effect could be generated by a large single object occupying the peripheral visual field and that a small bias towards the periphery existed even when the stimulated areas in the
central and peripheral parts of the visual field were equated. Finally, we found that the effect could be obtained even with face images, which are the non-optimal stimulus for these regions. Thus we concluded that building-related regions manifest a true retinotopic bias towards the peripheral visual field.

The results so far are compatible both with a smooth topography of object representations along the eccentricity axis and with a modular organization of object categories which is "super-imposed" on an eccentricity-biased map. To distinguish between these possibilities we mapped the representations of head images in front and back views, reasoning that these two image types engage related recognition processes on one hand, but impose different resolution needs on the other hand. We obtained activations of highly overlapping yet slightly offset regions in the fusiform gyrus. Crucially, the direction of this displacement was consistent across subjects and therefore could not be attributed to random variability. Such an activation pattern is not compatible with a modular organization, in which we would expect either no overlap or complete overlap of the active regions. Rather, this pattern reflects a continuous topography, in which representations of related objects "slide" smoothly along the fusiform gyrus.

In the last study we linked the fMRI signal to the underlying neuronal activation and obtained a lower bound estimate for the number of neurons participating in the representation of a single object. V1 fMRI and physiological data were first used to calibrate the ratio between neural activation and the fMRI signal. This ratio, in addition to several cautious assumptions, was applied to the fMRI signal in occipito-temporal cortex to estimate the neural activation to a single object. We found that at least a million neurons in object-related cortex are involved in the representation of a single object image, implying a highly distributed representation.
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Chapter 1  
**General Introduction**

### 1.1 The primate visual system

The primate visual cortex is an extremely complex system, comprised of many different areas, which are reciprocally connected. Anatomical, physiological and lesion studies in macaque monkey revealed more than 30 distinct areas in its visual cortex (Felleman and Van Essen, 1991). The recent advent of imaging methods in addition to electrophysiological and neuropsychological methods allow a similar mapping of the human visual cortex, and so far more than 10 areas have been identified (Tootell et al., 2003). Cells in different areas differ in their functional properties and in their cytoarchitectonics (Van Essen et al., 2001). The structure of the visual system is largely hierarchical, such that higher areas perform a progressively more complex analysis of the visual input. The first stage in this hierarchical structure is the primary visual cortex, V1, whose cells respond to oriented bars which appear in their receptive field. Each cell responds to a specific orientation in a relatively small part of the visual field (Hubel, 1988).

From V1 information flows into two anatomically segregated and functionally specialized streams (Ungerleider and Mishkin, 1982; Haxby et al., 1991; Ungerleider and Haxby, 1994): the dorsal stream which largely mediates spatial processing, such as position and direction of motion, and the ventral stream which deals primarily with aspects of object processing, such as shape and color. The highest stage in the ventral stream, the occipito-temporal cortex, is the focus of this thesis. While early visual areas in both dorsal and ventral streams are driven by relatively simple stimuli in specific visual field locations, activation of cells in high order areas in the ventral stream requires
complex stimuli (Malach et al., 1995; Tanaka, 1996), but is indifferent to the stimulus exact location (Grill-Spector et al., 1999).

1.2 Retinotopic areas

Early cortical visual areas are retinotopically organized. The visual information reaching the retina is transferred in an orderly manner to the Lateral Geniculate Nucleus (LGN) and from there to the primary visual cortex (V1). This topographic transformation from the retina to the cortical surface has been extensively studied both in non-human primates (Gattass et al., 1981; Gattass et al., 1988; Tootell et al., 1988) and more recently in humans, using functional magnetic resonance imaging (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997). These studies show that the Euclidean coordinate system in the retina is transformed into a polar coordinate system in the visual cortex. Thus, the visual field is mapped along two orthogonal axes: polar angle and eccentricity, where the system origin is at the fovea. Retinal points that lie on a circle whose center is the center of the visual field are mapped onto a straight band in V1. Points lying on a circle of a different radius are mapped onto a parallel band. From V1 the information is processed in higher and higher stages in the hierarchy: V2, VP and V4/V8 in the ventral stream (Hadjikhani et al., 1998) and V2, V3, V3A and possibly V7 in the dorsal stream (Tootell et al., 1997; Press et al., 2001). All these areas contain orderly maps of the visual field in polar coordinates, similar to V1. The polar angle axis reverses when crossing from one area to another: in V1 the map starts with the horizontal meridian and ends with the vertical one, in V2 a mirror representation starts with the vertical meridian and ends with the horizontal one, in VP the map reverses again and so forth. The relative position of the vertical and horizontal meridians provides an accurate delineation of the borders of these areas (Fig. 1A) (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997).
Contrary to the polar angle axis, a single eccentricity axis unites all the retinotopic areas into one entity (Fig. 1B), such that the iso-eccentricity bands are continuous across these areas.

Crucially, visual information processing changes along the eccentricity axis. This differential processing starts at the retina: the density of retinal neurons responding to the central visual field is highest and is reduced progressively when moving towards the periphery. In the cortex this difference translates into a logarithmic inverse ratio between the eccentricity of a unit distance on the retina and the amount of tissue dedicated to its representation (the magnification factor). Consequently, foveal regions are characterized by an extremely large cortical magnification (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997). This dramatic increase in magnification factor indicates a profound foveal specialization for the analysis of fine, high resolution, detail. In contrast, peripheral parts of the retina are mapped coarsely on the cortical surface, so that large visual field distances are mapped on relatively nearby points in the cortical surface.
1.3 Object-related areas

Anteriorly to the early visual areas described above lies a large expanse of cortical surface comprised of more high order and less topographically organized visual areas (Fig. 2). In recent years the newly developed neuroimaging techniques, particularly PET and fMRI, have begun to dissect these areas and to characterize them. A series of studies using these techniques revealed object-related activation in occipito-temporal cortex (Grill-Spector, 2003a). Several early PET studies identified ventral-temporal activation related to object and face recognition (Haxby et al., 1991; Sergent et al., 1992; Kosslyn et al., 1994). One of the early fMRI findings in this field was made by Malach et. al. (Malach et al., 1995). They have identified a large cortical region, located at the lateral and ventral aspects of the occipito-temporal cortex, which was termed the lateral-occipital complex (the LOC). This region showed preferential activation to a variety of complex object shapes, including faces and abstract 3D forms, compared to a large array of textures and noise patterns. Similar results were also obtained by Kanwisher et al (Kanwisher et al., 1996).

Anatomically the LOC was subdivided into two tentative entities: a more dorsal region, termed lateral occipital (LO), and a more ventral region along the posterior aspect of the fusiform gyrus (pFs). Further research expanded the extent of object-related cortex towards the Collateral Sulcus (CoS) ventrally (e.g. (Aguirre et al., 1998)) and the Intraparietal Sulcus (IPS) dorsally (e.g. (Haxby et al., 1999)).
1.3.1 Functional properties of object-related areas

Object-related areas exhibit the perceptual constancy required for a role in object-recognition. They are activated when subjects view an object shape, regardless of its physical properties. This shape can be defined by luminance, texture or motion cues (Grill-Spector et al., 1998a), as well as by stereo cues (Gilaie-Dotan et al., 2002), and the neuronal activation is independent of object format (gray-scale or line drawing, (Kourtzi and Kanwisher, 2000)). Convergence of bi-modal cues was recently demonstrated in a sub-region within occipito-temporal cortex. This region responded to tactile objects (Amedi et al., 2001) but not to auditory ones (Amedi et al., 2002).
Several findings indicate that object-related regions represent global shapes, rather than local features. Different local contours that produce similar percepts (occluded versus non-occluded shapes) produce similar activation in object-related areas, whereas similar local contours that generate different percepts (scrambled occluded versus occluded) produce different levels of activation in these areas. Kourtzi and Kanwisher (Kourtzi and Kanwisher, 2001) used fMR adaptation (Grill-Spector and Malach, 2001) to explore this issue at the neuronal level. They found that adaptation is observed when objects have the same shape but different contours, but not when contours are identical and the perceived shape is different.

At least part of the object-related cortex shows substantial invariance to objects' size and position (Grill-Spector et al., 1999), as well as contrast (Avidan et al., 2002b). Opposing results were obtained regarding the level of invariance to rotation around the vertical axis (Grill-Spector et al., 1999; James et al., 2002; Vuilleumier et al., 2002), possibly due to the different ranges of rotation angles used.

Finally, activation of object-related areas is closely related to recognition performance. Unrecognizable degraded objects elicit no activation, but once a perceptual cue helps to identify them activation is observed (Dolan et al., 1997). The level of activation in LO and pFs is correlated with percentage of correct response (Grill-Spector et al., 2000; Avidan et al., 2002b; Gilaie-Dotan et al., 2002) and a correlation with subjects' confidence in their response was reported in an anterior focus of fusiform gyrus (Bar et al., 2001).

These properties indicate that the LOC is a high order cortical region, which shows substantial specialization for object representations (Grill-Spector et al., 2001).
1.3.2 Category-related regions

Recent studies identified a large number of subdivisions within occipito-temporal object-related cortex which show preferential activation to certain object categories compared to others. The main examples of such categories are faces and building and scenes.

Several PET and fMRI studies identified a region in the posterior fusiform gyrus (pFs) which was activated by face images (Sergent et al., 1992; Haxby et al., 1994). Kanwisher et al (Kanwisher et al., 1997) showed that this region, termed the Fusiform Face Area (FFA), was activated at least twice as strongly for faces as for assorted objects. Several other studies demonstrated the preference of the FFA for faces over a variety of other categories (Puce et al., 1996; Halgren et al., 1999; Ishai et al., 1999). In addition to the FFA, face-related activation was also observed in the vicinity of the Inferior Frontal Gyrus (IOG) (Haxby et al., 1999; Hoffman and Haxby, 2000; Hasson et al., 2001) and in the Superior Temporal Sulcus (STS) (Hoffman and Haxby, 2000). Selective responses to faces were also observed using EEG (Bentin et al., 1996), MEG (Liu et al., 2000) and direct electrical recordings from the brain surface (Allison et al., 1999).

Following the discovery of face-related activation, selective activation to buildings and scenes was also reported. A region in the vicinity of the Collateral Sulcus was shown to be preferentially activated by buildings and landmarks compared to faces and other object categories (Aguirre et al., 1998; Haxby et al., 1999; Ishai et al., 1999). At the same time, an adjacent region in the parahippocampal gyrus was shown to be primarily active to outdoor scenes, but also to other images, provided that they contained information regarding the layout of local space (Epstein and Kanwisher, 1998).
Finally, specific activation patterns to other object categories such as words (Puce et al., 1996), tools (Martin et al., 1996), animals (Martin et al., 1996), human body (Downing et al., 2001) and chairs (Ishai et al., 1999) have also been reported.

1.3.3 Organization of object-related areas

Different object categories differ in many parameters, including shape factors, task-related factors and visual expertise effects. Hence, several organizational principles can account for the category-specific specializations found in occipito-temporal object related regions.

The first explanation is that the organization is based on semantic categories, i.e. each semantic category, like faces, houses, tools etc. will be represented in a separate cortical region. Such organization might be optimal since different object categories probably necessitate different specializations in their representations. Assuming a distinct cortical area for every object category is unreasonable, since the number of possible categories is infinite, but it is possible that only a limited number of categories are represented in separate regions, whereas all other objects are represented in a common area. A recent study (Downing et al., 2001) indeed claimed that only faces, places and body parts are represented in unique regions, whereas a large number of other tested categories did not exhibit such a selectivity.

A second possible explanation is that objects from different categories, e.g. a face and a house, look differently. They have different overall shapes, dissimilar typical features and different spatial relationships between these features. Conversely, different exemplars of a single category usually share similar features and contours. If similar features are represented by neighboring neurons
(Fujita et al., 1992), then objects that are visually similar could activate the same object-related cortical regions.

Different object categories are also different in their use. For example, buildings and landmarks are used for spatial navigation, faces have a crucial role in social interaction and tools are used to manipulate other objects. Thus, a third explanation would be that object representations are organized according to the most common tasks they are used for. Such organization could facilitate optimal connectivity to higher level, action-related centers.

An additional dimension along which object categories differ is the level of expertise we have with each category. Expertise is demonstrated by the ability to recognize an individual exemplar within a category, and is associated with an extensive visual experience with that category. A fourth possible explanation is that the organization of object representations is based on the degree of expertise associated with each category (Tarr and Gauthier, 2000). Since all humans are experts in face recognition, it could be that the face-related area is actually an area of expertise. Indeed, it was found that subjects trained to recognize novel objects ("greebles") on an individual level had enhanced activation in their face-area to these objects (Gauthier et al., 1999). Similarly, bird and car experts had enhanced activation in their face area to birds and cars respectively (Gauthier et al., 2000). These findings are not devoid of caveats. The "greebles" used in the first experiment were very reminiscent of animate creatures, their spatial configuration was face-like and subjects were trained to identify them using proper names, which could have induced a human interpretation (Kanwisher, 2000). The results of the second experiment are stronger, but may in part reflect a general arousal effect the category of expertise had on the subjects. Still, the
expertise factor cannot be ruled out as underlying the differential activity to different object categories.

Finally, a completely different view is that objects are represented in a distributed activation pattern across all ventral cortex (Haxby et al., 2001). This is compatible with neuroimaging results in which the preference of a specific category is always relative rather than absolute, such that each region shows substantial activation to the non-preferred categories (Malach et al., 1995; Ishai et al., 1999). Haxby et al showed that the distinct activation pattern to eight different categories is replicable, and that the object category can be predicted based on the activation pattern even if regions showing the maximal activation to a particular category are excluded. Spiridon and Kanwisher (Spiridon and Kanwisher, 2002) replicated the results, but showed that areas of maximal activations for faces and places are not useful in discriminating between non-preferred categories. Using adaptation as a measure of activation level, Avidan et al (Avidan et al., 2002a) demonstrated the existence of building-selective neurons in the pFs face-related region and vice versa, supporting the notion of a more distributed nature of object representation.

While all of the above mentioned principles may account for the differential activation patterns elicited by different object categories, they leave two questions unanswered. First, none of the suggested principles explains the consistent neuroanatomical relationships between regions of category-related activation across subjects and studies. For example, despite substantial inter-subject variability the preferential activation to faces is invariably located in the vicinity of the fusiform gyrus, laterally to the activation to building images, which lies in the vicinity of the collateral sulcus. Second, the exact nature of the neuronal representation is not clear. Specifically, the number of neurons participating in the representation of each object is not known. Different theoretical models vary substantially in their assumptions regarding this number, ranging between
very few "grandmother cells" (Konorski, 1967) and very large distributed networks (Shadlen and Newsome, 1998).

1.4 Thesis outline

The primary goal of this thesis was to find an overall underlying principle that will explain the different activation patterns to different categories and their consistent anatomical location. The approach of previous studies looking for such principles was mostly cognitive and focused on the functional properties of object-related regions. We employed a neuroanatomical approach by exploring how the topography of object representations is related to the overall organization of the visual cortex.

In chapter 2.1 (Levy et al., 2001) we report a unifying principle underlying the organization of object-related areas. We show that these areas are organized according to visual field eccentricity biases, extending the robust eccentricity organization of early visual areas. We also show an association between object categories and certain eccentricity biases. Specifically, faces were associated with the center of the visual field, whereas buildings were associated with the periphery. In chapters 2.2 and 2.3 we further explore the nature of the center-periphery organization. First, in chapter 2.2, we examine the relationship between the two dimensions found in occipito-temporal cortex: object category and eccentricity. In addition we investigate the exact nature of the peripheral bias found in building-related areas. Then, in chapter 2.3, we examine the nature of the face-area and whether the representation of faces is modular or continuous. Finally, in chapter 2.4 we construct a framework for using the fMRI signal to assess a lower bound for the number of neurons participating in the representation of a single object.
Chapter 2

Results

2.1
Center-periphery organization of human object areas

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Center-periphery organization of human object areas

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The organizing principles that govern the layout of human object-related areas are largely unknown. Here we propose a new organizing principle in which object representations are arranged according to a central versus peripheral visual field bias. The proposal is based on the finding that building-related regions overlap periphery-biased visual field representations, whereas face-related regions are associated with center-biased representations. Furthermore, the eccentricity maps encompass essentially the entire extent of object-related occipito-temporal cortex, indicating that most object representations are organized with respect to retinal eccentricity. A control experiment ruled out the possibility that the results are due exclusively to unequal feature distribution in these images. We hypothesize that brain regions representing object categories that rely on detailed central scrutiny (such as faces) are more strongly associated with processing of central information, compared to representations of objects that may be recognized by more peripheral information (such as buildings or scenes).

During natural viewing, certain objects (such as faces) require detailed central scrutiny to perform such subtle visual tasks as detecting facial expressions and eye-gaze directions. Larger objects (such as buildings or scenes) occupy a more peripheral field location, and can be recognized by their more peripheral-shape information. This distinction is further illustrated by the tendency of scanning eye movements to fixate face parts rather than background objects. However, the potential role of this distinction in the organization of object representations has not been addressed so far.

Early visual areas of primates are retinotopically organized, so that the visual field is mapped in each area along two orthogonal axes: polar angle and eccentricity. The center/periphery organization, that is, eccentricity mapping, is one of the most striking and robust organizational principles in the primate visual cortex. Both monkey and human cortices exhibit a meta-structure of center-periphery organization, in which similar distances from the fovea are mapped in stripes that are continuous across the entire ensemble of retinotopic visual areas. The center/periphery organization extends into higher-order visual areas, whereas the polar angle representation in these areas is cruder, and orderly representations of the visual field meridians are absent. Despite the evident importance of eccentricity maps, their possible relationship to object recognition has received little attention, and the possible effect of this organization on the way different object categories are represented in the human brain has not been studied.

Recently, the distinction between representation of faces and buildings has become a central issue in human visual cortex studies, due to the discovery that clearly distinct cortical regions are differentially activated by the two image categories: buildings activate a medial region along the collateral sulcus/parahippocampal gyrus, whereas faces activate a neighboring, more lateral region along the posterior fusiform gyrus. The segregated representation of these object categories was attributed by some authors to task- or semantics-related specialization, and by others to the particular geometric information.

Here we report on an association between the two functional organizations found in human visual cortex: eccentricity maps and object categorization. Thus, we found that face-related regions are associated with central visual field representations, whereas building-related regions are associated with peripheral field representations. Furthermore, the center-periphery organization seems to encompass the entire constellation of high-order human object areas. Within the center-periphery maps, we found a hierarchical-like organization in that posterior regions manifested higher retinotopic bias compared to more anterior regions. Thus, our results unify two sets of findings in human visual cortex, eccentricity mapping and object selectivity, into a global principle of organization.

Results

To explore the potential relationship between eccentricity maps and object selectivity, we first located face-related and building-related regions in the human visual cortex (experiment 1A). These regions were then superimposed onto the representation of visual field eccentricity in each subject (experiment 1B). To increase the sensitivity of high-order object areas to the visual field mapping, we constructed the retinotopic stimuli from a variety of natural object images (Fig. 1, see Methods). We also mapped the horizontal and vertical visual field meridians that delineate borders of retinotopic areas and superimposed the object areas on them.
Results

Typically, face-related voxels were found in two foci (Fig. 2a and b): the lateral occipital region (LO) and the posterior fusiform gyrus (pFs). LO is situated ventrally and posteriorly to MT, extending into the posterior inferotemporal sulcus. Region pFs is anterior and lateral to areas V4/V8 (ref. 22), extending into the occipitotemporal sulcus, and corresponds to the fusiform face area (FFA) described previously16. Both foci largely overlapped the representation of the visual field center (Fig. 2c, yellow). Building-related voxels were found mainly in the collateral sulcus, where they partially overlapped an upper meridian representation and extended beyond it (Fig. 2a and b). This region largely overlapped the peripheral visual field representation (Fig. 2c, green) and sometimes extended to the mid visual field representation (Fig. 2c, purple), but always avoided the central field representation. Building-related voxels were also found in a dorsal region, in the vicinity of V3A and V7, where they often tended to overlap the periphery and mid representations.

In all the face-related regions, activation was significantly stronger in response to central stimuli compared to mid and peripheral stimuli (Fig. 3). LO, center versus periphery, p < 0.005, center versus mid, p < 0.005, n = 12, one-tailed paired t-test; pFs, center versus periphery, p < 0.005, center versus mid, p < 0.05, n = 11, one-tailed paired t-test). In analyzing the building-related regions, we included only voxels that both were selective to buildings compared to faces, and were anterior to areas V4/V8 (Fig. 2b). This region exhibited a high preference to the peripheral visual field representation compared to the central and mid ones (Fig. 3). Anterior CoS, periphery versus center, p < 10^-5, periphery versus mid, p < 10^-5, n = 12, one-tailed paired t-test).

To test the relationship between eccentricity and object categorization directly, we conducted another experiment, in which we mapped both center versus periphery and buildings versus faces during one scan (experiment 2). In the center and periphery conditions of this experiment, subjects viewed the exact same objects (see Methods), such that the two conditions only differed in the part of the visual field stimulated by the images and not in their shape features.

Again, face-related voxels were found in LO and in the pFs, where they overlapped the representation of the visual field center to a large extent, and building-related voxels were found mainly in the collateral sulcus, where they largely overlapped the peripheral visual field representation (Fig. 4a).

The Talairach23 coordinates of the face- and building-related regions (Table 1) showed that our maps were in close correspondence to previous reports (buildings:11, 13, 24, faces:15, 16, 25). The white circle in Fig. 2b shows the approximate position of face-related regions reported in early studies.

To make sure that subjects were able to recognize the objects in the peripheral stimuli, we conducted a behavioral experiment in which subjects were required to name the central and peripheral stimuli from experiment 2. The results showed that under the specific task of that experiment, there was a slight trend toward better recognition of objects in the center (mean ± s.d., 91 ± 7% correct responses) compared to the periphery (86 ± 9% correct responses).

Thus, it is clear that a consistent association exists between the representation of particular object images and the central versus peripheral representation. However, it should be emphasized that the object representations were not homogenous: a clear indication of a hierarchical trend was observed, in that more posterior regions manifested a higher eccentricity bias compared to the most anterior regions. Thus, all face-related areas exhibited a significant central bias (Fig. 4b). LO, p < 0.0005; pFs, p < 0.05, n = 5, one-tailed paired t-test, center versus periphery). However, face-related foci located in LO showed a significantly higher central bias than those located in pFs. The ratio between activation to the

Fig. 1. Stimuli used to map object-selective areas and eccentricity representations (experiments 1A and 2). Examples of stimuli used to map the face- and building-related areas and the center and periphery representations (see Methods for details). The center stimulus shown here was enlarged four times compared to the actual experiment, for presentation purposes.
center and periphery conditions was significantly higher in LO than in pFs (p < 0.02, one-tailed paired t-test). Activation ratio in the most anterior part of the face region in each subject (up to 3 voxels) was not significantly different from the ratio in the entire pFs (p = 0.1). The building-related area exhibited high preference to the peripheral visual field representation (Fig. 4b, p < 0.002; n = 5, one-tailed paired t-test). Comparing the center/periphery ratio between the entire area and its most anterior part (up to 3 voxels), showed no significant difference (p = 0.1).

The association of faces and buildings with central and peripheral representations may have emerged from the retinal center/periphery distribution of features in face and building images; for example, building images may tend to contain more low-level visual features such as edges and corners in the periphery than in the center. To test this possibility we conducted another experiment (experiment 3), in which subjects viewed pictures of buildings and faces as in experiment 2 (Fig. 5, ‘regular’), but also pictures of larger faces and smaller buildings. These images were aimed at increasing the density of visual features in the periphery in the case of faces, and decreasing it in the case of buildings (Methods, Fig. 5). We compared the spectral energies of the central and peripheral parts of the images in each category (Methods, Fig. 5) and found that in the peripheral part of the visual field, the big-faces spectral energy was indeed higher than the energy of the small buildings.

As expected, in low-level retinotopic areas, which contain orderly representations of vertical and horizontal meridians (dotted lines in Fig. 6a), the activation pattern followed the retinal feature distribution in the images. Thus, ‘large-face’ selective voxels tended to overlap more peripheral field representations (green) compared to ‘small-building’ selective voxels, which activated more central representations (yellow). However, this trend was inverted in more anterior regions, outside the early retinotopic areas: the large-face selective voxels here overlapped central visual field representations, whereas the small-buildings were associated with peripheral field representations.

Another way to analyze this experiment is to select voxels that were preferentially activated by regular faces compared to regular buildings and those that exhibited the opposite preference, and to examine their activation in response to large faces and small buildings (which were both ignored in the statistical tests). This analysis showed that face-related voxels were also activated by large faces (mean ± s.e.m., 1.4 ± 0.1%) more than by small buildings (0.6 ± 0.1%; p < 0.001, n = 6, one-tailed paired t-test), whereas building-related voxels were activated by small buildings (0.9 ± 0.1%) more than by large faces (0.4 ± 0.1%; p < 0.005; Fig. 6b). Overall, these results clearly rule out the possibility that the center/periphery bias of faces and buildings is due to a difference in the retinal distribution of features in the images of these objects. However, voxels in the anterior collateral sulcus, which were preferentially activated by buildings compared to faces, also showed somewhat higher activation to large faces compared to regular ones. This preference can be expected from the peripheral visual field bias observed in this region.

To what extent can the center-periphery organization be extended to other object categories? To delineate the entire expanse of object-related cortex, we used a diverse set of objects and compared the activation produced by it with that produced by texture patterns (experiment 1). This contrast was shown previ-
results

**Table 1. Talairach** coordinates of face-related and building-related regions.

<table>
<thead>
<tr>
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<th>Left hemisphere</th>
<th>Right hemisphere</th>
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<tr>
<td><strong>Faces</strong></td>
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Values are mean ± s.d. in mm.

Discussion

**Center–periphery organization in human object areas**

Our results reveal an association between object images and the organization of visual field eccentricity. Thus, in high-order object areas, both large and small face images tended to be associated with central visual field representations (Figs. 4a and 6a, red), whereas both large and small building images tended to overlap peripheral field representations (Figs. 4a and 6a, blue). This association cannot be attributed to irregular mapping results, because both our maps of face and building-related regions, as well as our maps of central versus peripheral visual field representations, closely correlate with previously reported maps (faces13–16,18,24,25,27, buildings11,13,24, center/periphery5,22).

The finding of an eccentricity map in high-order object areas extends the previous report by our group of a foveal bias in the LOC26. The extension of the eccentricity maps to areas beyond the already characterized retinotopic areas18,22 is most likely due to the use of object stimuli in the eccentricity mapping, rather than the texture-like stimuli typically used in earlier studies. Textured stimuli have been shown to be largely ineffective in activating high-order object areas26.

Macaque IT, which was suggested to be homologue to human LOC, has been shown to exhibit object selectivity25,30 and to manifest a foveal bias15,31–34. A suggestion for a center/periphery segregation, compatible with the one described here, was found in posterior IT, in which the central visual field was represented more dorsally, and the peripheral visual field more ventrally10,35. However, these studies did not compare the feature/object selectivity in these regions, so it is unclear whether macaque IT actually exhibits an association between visual field and object selectivity similar to the one found here.

Although our results clearly point to a central versus peripheral bias in object-related, high-order areas, these regions did not exhibit a well-organized visual meridian representation4,7,20 which is characteristic of early retinotopic areas. This result is again compatible with response properties of monkey IT neurons19,35 as well as other neuroimaging results (for example, see ref 18).

**A consequence of the physical distribution of features?**

The central versus peripheral bias we observed could not be explained as a simple consequence of a center/periphery imbalance in the statistical distribution of visual features present in the face and building images used in our experiment. The relationship of faces and buildings to eccentricity maps was maintained even when the center/periphery balance of features was substantially modified by changing image size (Fig. 5; compare the spectral energy of the large faces and the small buildings). The peripheral bias did manifest itself in an enhancement of the activation for both buildings and faces when these were increased in size (Fig. 6b); however, this enhancement was not sufficient to overcome the shape-selective, preferential activation for buildings over faces characteristic of this region.

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**Fig. 5.** Stimuli used in experiment 3. Average spectral energy of the central (top) and peripheral (bottom) parts of the images in each category of experiment 3. Energy was calculated as the sum of squares of amplitudes in the range 0.1–9 cycles/degree, in each image part: y-axis, normalized energy (see Methods). Error bars, s.d. In the peripheral part of the visual field, the energy in large face images was higher than the energy in small buildings.
Potential confounds

Additional factors that could have affected the results are attentional effects and eye movements. Attentional level was maintained across the various experimental conditions by using an identical task of equal attentional demand (1-back memory task) throughout the experiment (see experiment 1A, Methods). The clear retinotopy observed in our retinotopic and eccentricity maps rules out major eye movements during the scans. In addition, we obtained similar results using brief (250-ms) image presentations, which prevented extensive scanning eye movements (see experiment 2, Methods). Thus, our results cannot be attributed to differential eye movement in the different conditions.

In summary, our results unite two seemingly unrelated organizational features of human visual cortex, eccentricity maps and object selectivity, into a global organization in high-order occipito-temporal cortex.

Putative sources for the center-periphery organization

Such a center/periphery organization may have a developmental basis. During the layout of object representations, object categories are associated with the region of visual space that is attended during the establishment of these representations. Because faces require central scrutiny, possibly due to the minute differences in features that are critical for recognition, they are associated with a central field bias, whereas buildings will be associated with a peripheral bias. In relation to this, expertise training in recognition of specific objects (for example, birds) leads to enhanced activation in face-related (and by implication, center-biased) cortical regions.25,36

A complementary explanation is that the center/periphery organization allows for a more efficient allocation of processing resources for different object categories. Objects whose identification necessitates high acuity will receive more extensive inputs from the foveal representation, which provides the needed spatial resolution. In contrast, objects that can be recognized at a coarser level or that require large-scale integration of features will be associated with more peripheral representations. We would thus anticipate that representations of letters and digits (for example, refs. 14, 37), which strongly depend on foveal vision, will be associated with central field representations. We are currently exploring this prediction.

Results

Fig. 6. Experiment 3, feature distribution experiment. (a) Results of experiment 3 in the right hemisphere of one subject. Red, voxels preferentially activated by large faces compared to small buildings; blue, voxels preferentially activated by small buildings compared to large faces. Left, object-selective areas superimposed on retinotopic borders, which are denoted by dotted lines. Color scales indicate the degree of statistical correlation. Right, the same areas superimposed on the eccentricity representation (yellow, center; green, periphery). Dotted line, estimated anterior border of retinotopic areas. Outside the retinotopic areas, the large-face voxels overlapped the central visual field representation, whereas the small buildings were associated with the peripheral field representation (indicated by arrows). (b) Average signal from the six subjects who participated in experiment 3. Left, voxels selected by applying a statistical test that searched for preferential activation for regular faces compared to regular buildings. Error bars, s.e.m. Right, voxels selected by applying the test ‘regular buildings > regular faces.’ Error bars, s.e.m. Large faces and small buildings were not included in the voxel selection test, and only voxels that were outside retinotopic areas were included in the analysis. The charts show that face-related voxels were also preferentially activated by large faces, and building-related voxels were also activated by small buildings.

Fig. 7. Large-scale relationship of object-related cortex with center–periphery organization. (a) Preferential activation to objects versus patterns (red) and to patterns versus objects (blue) from 13 subjects (experiment 1). The results are presented on an inflated brain, shown in a ventral view (left) and on the unfolded hemispheres (right). Abbreviations as in Fig. 2; STS, superior temporal sulcus; PHG, parahippocampal gyrus. (b) Eccentricity maps from 12 subjects presented on an inflated brain shown in a ventral view (left) and on the unfolded hemispheres. Yellow, center; purple, mid; green, periphery. The borders of object areas from (a) were superimposed on the unfolded eccentricity map (red). Most of the object-related regions, with the exception of a few anterior foci, were contained within the center–periphery organization. Color scales indicate statistical correlation.
Relationship to other object categories?
Although we present data here regarding only two specific categories, buildings and faces, our results are also relevant to other object categories. This conclusion stems from the finding that substantial overlap occurred between the extent of object-selective occipito-temporal cortex and the center/periphery eccentricity maps. The implication of this large-scale correspondence is that any object category will have to be mapped somewhere along the eccentricity dimension and consequently will be associated, to some extent, with a particular combination of ‘preferred’ eccentricities.

The fact that different object classes are mapped according to a center/periphery rule does not exclude the possibility that additional stimulus dimensions may be mapped in an orderly manner within this cortical expansion. Clearly, the face-related voxels do not overlap the entire center-biased regions, leaving room for other possible object categories. Similarly, various category-specific subdivisions may occur within the periphery-biased representation of the collateral sulcus (for example, Epstein and Kanwisher[19]).

Hierarchical organization within human object areas
The center-periphery organization described here provides a unified organizing principle for the entire extent of occipito-temporal, object-related cortex. However, this cortical expansion is not uniform. In particular, the more dorsal-posterior face-related regions seem to show a higher degree of central-field bias compared to the more ventral-anterior parts in the posterior fusiform gyrus (pFs), although the pFs did show a significant central bias (Figs. 3 and 4b), which was particularly evident when compared to the neighboring, peripherally biased collateral sulcus.

A similar hierarchical trend was also observed along the anterior-posterior axis of the collateral sulcus as one moves from V4/V8 toward the more anterior part of the sulcus. These results are compatible with our previous reports of a differential position and size selectivity within the LOC, whereby posterior regions showed a higher degree of sensitivity to these changes compared to anterior regions.

Following the acceptance of this work, a paper appeared[18] showing a center/periphery organization in dorsal LO using checker-board stimuli—thus providing additional confirmation to the prevalence of this organization in high-order visual areas.

Methods
Subjects.
Fourteen healthy subjects (8 women, 24–49 years old), participated in one or more of the experiments. 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 acquisition.
Subjects were scanned on a 1.5 Signa Horizon LX 8.25 GE scanner equipped with a quadrature surface coil (Nova Medical, Wakefield, Massachusetts), which covered the posterior brain regions. Blood oxygen 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 cm²; matrix size × 80 × 80). The scanned volume included 17 nearly-axial slices of 4-mm thickness and 1-mm gap.

The weighted high resolution (1 × 1 × 1 mm) anatomical images and a three-dimensional SPGR sequence were acquired for each subject to allow accurate cortical segmentation and reconstruction, and volume-based statistical analysis.

Visual stimuli.
Stimuli were generated on a PC, projected onto a tangent screen positioned in front of the subject’s forehead, and viewed through a tilted mirror.

Experiment 1. This experiment comprised two separate scans. In the first scan (experiment 1A), areas that showed preferential activation to common objects, faces or buildings were located (‘objects scan’), and in the second scan (experiment 1B), eccentricity maps were obtained (‘eccentricity scan’). Thirteen subjects participated in this experiment. The eccentricity scan of one subject was excluded due to problems in data acquisition.

In the objects scan (1A) subjects were presented with black and white drawings of faces, buildings, common objects and texture patterns shown in seven 9-s blocks of each category. The blocks were pseudo-randomly ordered and alternated with 6-s blanks. Each block consisted of 9 pictures, randomly ordered. The experiments included either 64 or 32 different pictures (4 and 9 subjects respectively). Each picture was presented for 800 ms followed by a blank interval of 200 ms. One or two pictures in each block were repeated, and subjects were asked to perform a ‘one-back’ matching task, while fixating on a central red point.

In the eccentricity scan (1B), subjects were presented with pictures of different 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). Three types of central stimuli were used in separate epochs: faces, common objects (mainly animals) and written words. Pictures were presented in 18-s blocks, in which each picture was presented for 250 ms. Subjects were requested to fixate on a small fixation dot. Visual epochs alternated with 6-s blanks. Four cycles of the stimuli were shown.

Experiment 2. This experiment was designed to simultaneously map object-selective activation and center–periphery visual field bias (Fig. 1). Five subjects participated in the experiment. Line drawings of faces and buildings were used to locate object-selective areas (black and white, visual angle 12° × 12°). For the center–periphery mapping we used colored drawings of a variety of common objects. In the ‘center’ epochs, the stimuli were located in a circle at the center of the visual field (diameter, 1.8°). In the ‘periphery’ epochs, a number of copies (12–13) of the same object were placed within a ring confined to the peripheral visual field (11.5° inner diameter, 20° outer diameter, Fig. 1). Pictures of faces and buildings were presented in six blocks of 9 s each. Each block consisted of 18 different pictures. Thirty-six pictures of each type were used throughout the experiment. Each picture was presented for 250 ms followed by a blank interval of 250 ms. Central and peripheral pictures were presented in five 18-s blocks, in which each picture was presented for 250 ms. Seventy-two pictures of each type were used throughout the experiment. The visual stimulation blocks were ordered pseudo-randomly and alternated with 6-s blanks. A red fixation point was positioned centrally throughout the experiment, and subjects were instructed to fixate on it.

Experiment 3: Feature distribution experiment.
Six subjects participated in this experiment. They were presented with pictures of faces and buildings as in experiment 2 (12° × 12°) and with two additional categories: large faces (same faces, enlarged to a size of 17.5° × 17.5°) and small buildings (same buildings reduced to a size of 5.8° × 5.8°). Sixteen pictures of each category were used. Presentation procedure and task were the same as in experiment 1A.

Behavioral experiment.
Six subjects participated in a behavioral experiment, which was conducted outside of the magnet six months after the fMRI scans. They were presented with the central and peripheral stimuli from experiment 2, and were asked to name them, while fixating on a red dot at the center of the screen. Each picture was presented for 250 ms followed by a 1250-ms blank. Percentages of correct responses were calculated.

Mapping borders of visual areas.
The representations of vertical and horizontal visual field meridians were mapped in all subjects in order to delineate borders of retinotopic areas[13,20,21]. Visual stimulation was presented in 18-s blocks. Each image was presented for 250 ms. The stimuli consisted of triangular wedges that compensated for the expanded foveal representation. The wedges were presented either vertically (upper or lower vertical meridians) or horizontally (left or right horizontal meridians). The wedges consisted of either gray-level natural images or black and white objects from texture pictures[26]. Subjects were requested to fixate on a small central cross. Visual epochs alternated with 6-s blanks. Four cycles of the stimuli were shown.
Data analysis. fMRI data were analyzed with the BrainVoyager software package (R. Goebel, Brain Innovation, Maastricht, Netherlands) and with complementary in-house software. Each subject’s data from each scan were analyzed separately (except for the multi-subject analysis, see below). The functional images were superimposed on two-dimensional anatomical images and incorporated into the three-dimensional data sets through trilinear interpolation. The complete data set was transformed into Talairach23 space. Preprocessing of functional scans included three-dimensional motion correction and high-frequency temporal filtering. Statistical analysis was based on the General Linear Model.4

The cortical surface was reconstructed from the three-dimensional SPM99 scan, unfolded, cut along the calcarine sulcus, and flattened. The obtained activation maps were superimposed on the unfolded cortex and the Talairach coordinates were determined for the center of each ROI.

To create the maps, the time courses of all subjects were transformed into Talairach23 space. Preprocessing of functional scans included three-dimensional motion correction and high-frequency temporal filtering. Statistical analysis was based on the General Linear Model.4

The two-dimensional Fourier transforms (FT) of the images in experiment 3 were calculated using the MATLAB software (Mathworks, Natick, Massachusetts, 1999) according to the following formula:

\[ X(u, v) = \sum_{j=0}^{N-1} \sum_{k=0}^{N-1} x(j, k) e^{2\pi i (uj + kv)} \]

Here, \( X \) is the FT, \( x \) is the image and \( N \times N \) is the image size.

FT was computed separately for the central part of each image and the peripheral part. The square amplitudes of frequencies between 0.1 and 5 cycles/degree in each image part were summed (total energy):

\[ E = \sum_{i=0}^{N-1} |A(i, j)|^2 \]

Here, \( E \) is the total energy and the summation is over the frequencies in the above range.

The bar charts in Fig. 5 present the mean total energy in the central and peripheral parts of each category, normalized by the regular faces total energy.

Multi-subject analysis. The object-areas map in Fig. 7 was obtained from 13 subjects. The eccentricity map was obtained from 12 of these subjects. To obtain the maps, the time courses of all subjects were transformed into Talairach space, z-normalized and concatenated, and the statistical tests were done on the concatenated time course.

Acknowledgements

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2.2
Functional analysis of the periphery effect in human building areas

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Human Brain Mapping (In-press)
**Abstract**

Several studies have shown that a region in the anterior collateral sulcus (CoS) and a region in the vicinity of the transverse occipital sulcus (TOS) are preferentially activated by images of buildings and scenes. We have recently found that these regions show a strong activation bias to stimuli located in the peripheral visual field. Here we explore in detail the source of this “periphery” effect. We addressed the following questions: First, is the periphery effect related to the number of objects presented? Our results show that the effect can be generated both by a large single object occupying the peripheral visual field as well as by multiple small peripheral objects. Second, is the periphery effect related to the annular shape used in conventional mapping of the visual field periphery? Our results show that the mere presence of a stimulus in the visual field periphery, regardless of object shape, is sufficient to enhance activation. Third, is the periphery effect due to the increased stimulated area rather than visual field location? Our results show a small bias towards the peripheral visual field even when the stimulated areas in the central and peripheral parts of the visual field are equated. Finally, does the periphery effect show object selectivity? Our results show that the effect can be obtained even with face images, which are the non-optimal stimulus for this region. In summary, our study shows that the building-related CoS and TOS manifest a true but graded retinotopic bias towards the peripheral visual field.

**Introduction**

The introduction of functional Magnetic Resonance Imaging (fMRI) of high order human visual areas, has revealed a highly elaborate and complex constellation of object-related regions in the
non-retinotopic occipito-temporal cortex, centered on the lateral occipital complex (LOC) (e.g. (Grill-Spector et al., 2001; Grill-Spector, 2003; Hasson et al., 2003)). A series of studies have demonstrated a striking differential selectivity along the ventral surface of the temporal lobe. While the lateral aspect of the fusiform gyrus manifests preferential activation to face images in a region known as the FFA (Puce et al., 1995; Kanwisher et al., 1997; McCarthy et al., 1997; Halgren et al., 1999; Haxby et al., 1999), the collateral sulcus (CoS) and the parahippocampal place area (PPA) show preferential activation to buildings and scenes (Aguirre et al., 1998; Epstein and Kanwisher, 1998; Haxby et al., 1999) (e.g. Fig. 1). Such high order object areas were considered to be largely non-retinotopic, since they show greatly reduced sensitivity to visual field location of the stimuli. For example, LOC regions show robust activation even to ipsi-lateral visual field stimulation, something which is absent in early visual areas (Grill-Spector et al., 1998; Tootell et al., 1998; Halgren et al., 1999).

However, recently we have found that some retinotopic dimension does appear to be preserved in these areas, as visual field eccentricity is represented differentially in the face compared to building related regions. Thus, we have found that building-related regions show a significantly greater activation to peripheral stimulation compared to face-related regions (Levy et al., 2001). More specifically, in the building related CoS, activation was higher to a peripheral ring containing multiple enlarged object copies compared to a centrally located single object (e.g. Fig. 2a). A similar result was obtained recently in a dorsal region in the vicinity of the TOS, which also exhibits a preference to building stimuli (Hasson et al., 2003). These results raise several questions regarding the nature of the periphery effect. First, it is of interest to find whether the effect, similar to the general activity in the CoS and the TOS, is object-selective, i.e. whether it is stronger for a certain class of objects compared to others. Specifically, we tested whether the periphery effect is
different for optimal versus non-optimal categories. Second, the observed periphery effect may be attributed to several alternative factors. One option is that the enhanced activation may not necessarily be due to the peripheral location of the stimuli, but rather to the annular shape that is conventionally used in the peripheral stimuli. Alternatively, since the peripheral ring included a number of repeating objects, it could be that activation in the CoS and the TOS simply reflects the number of objects presented rather than their peripheral location.

Finally, it could be that the observed peripheral bias was actually due to the enlarged area of visual field stimulation used to compensate for the magnification factor, rather than the visual field location, i.e. the activation may be directly proportional to the area of retinal stimulation. Here we report several results relevant to these aspects. Our study shows that the periphery effect is indeed related to the visual field periphery, and can be explained best as reflecting a process of large scale integration across the visual field.

**Results**

**Localizing building-related regions**

Building related regions were identified using an external localizer by contrasting the activation to building and face images. The obtained active regions which lay anteriorly to retinotopic areas were defined as regions of interest (ROI's) and subsequent analysis was confined to them. In all 17 subjects building-related activation was obtained in the ventral occipitotemporal cortex (VOT) in the vicinity of the CoS: in 15 subjects this activation was bilateral, in one subject it was confined to the right hemisphere and in another to the left hemisphere (Table 1). Fig. 1 shows the location of the building-related CoS in a typical case on an inflated brain in a ventral view and on a flattened brain.
This region corresponds to the building-related region described by Aguirre et al. (Aguirre et al., 1998) and extends into the Parahippocampal Place Area (PPA) described by Epstein and Kanwisher (Epstein and Kanwisher, 1998). Building-related activation was also obtained in the dorsal occipitotemporal cortex (DOT) in the vicinity of the transverse occipital sulcus (TOS), extending in some cases to the intra-parietal sulcus (IPS) and the lateral occipital sulcus (LOS), in agreement with previous results (Haxby et al., 1999; Hasson et al., 2003). A typical example can be seen in Fig. 1 on an inflated brain in a dorsal view and on a flattened brain. Such activation was found in 14 subjects: bilaterally in 13 subjects and in the right hemisphere of one subject (Table 1), but was weaker and more variable than the CoS activation.

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<th>Table 1: Talairach coordinates</th>
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Talairach coordinates of building-related regions. Values are mean ± s.d. in mm. n, number of subjects.
Figure 1: Building-related regions in a representative subject

Building-related regions (blue) presented on an inflated (top) and flattened (bottom) brain formats of a single subject. Building-related regions were defined in a localizer experiment by contrasting activation to building and face images. Preferential activation to faces compared to buildings (red) is shown for comparison. Blue arrows show the ROIs on which subsequent analysis was performed. Color scales indicate the significance of the statistical test. The inflated brain is shown in ventral (left) and dorsal (right) views. Dotted lines on the left flattened hemisphere denote borders between areas V1, V2, VP, V3, V3A, V4/V8 and MT, which are marked by white arrows. The CoS region of interest was defined as the region showing preferential activation to buildings in the vicinity of the CoS, anteriorly to V4/V8. An additional region was located in the vicinity of the TOS and the LOS, anteriorly to V3A. L, left; R, right; Ant, anterior; Post, posterior; CoS, collateral sulcus; IPS, intra-parietal sulcus; ITS, inferior temporal sulcus; LOS, lateral occipital sulcus; OTS, occipito-temporal sulcus; PCS, post-central sulcus; POS, parieto-occipital sulcus; STS, superior temporal sulcus; TOS, transverse occipital sulcus.
Experiment 1 – mapping the periphery effect with a single category

The basic periphery effect reported previously in the CoS was obtained using a mixture of different objects (Levy et al., 2001). The first question we addressed here was whether the periphery effect is category-dependent. Thus, in experiment 1 we used face and building images, shown either in the center or in a peripheral ring (Fig. 2a, see also (Hasson et al., 2002)). As expected, this region manifested a clear preferential activation to building images compared to face images (building-center vs. face-center, p<0.02, one-tailed t-test, n=9) and a clear bias toward the peripheral ring of objects compared to the central object stimulus (Fig. 2b). Importantly, this peripheral bias was obtained for both object categories (building-periphery vs. building-center, p<0.05; face-periphery vs. face-center, p<0.001). In fact, face images showed a slightly stronger periphery bias compared to that produced by building images, despite the fact that they were suboptimal stimuli when presented at the center (face periphery-bias: 0.8±0.1 mean±SEM; building periphery-bias: 0.3±0.2; face periphery-bias vs. building periphery-bias, p=0.07, two-tailed t-test). The source of the periphery effect for faces appeared to be the substantial reduction in building selectivity when the object images were presented in the peripheral location. Although a slight bias towards building stimuli was observed, it did not reach significance (building-periphery vs. face-periphery, p=0.14).

Similar results were obtained in the TOS (Fig. 2c): this region exhibited a preferential activation to buildings when presented in the center (building-center vs. face-center, p<0.02, n=9), but not in the periphery (building-periphery vs. face-periphery, p=0.18) and also showed a periphery-bias, which was significant in the case of buildings and approached significance in the case of faces (building-periphery vs. building-center, p<0.005; face-periphery vs. face-center, p=0.05).
Figure 2: Experiment 1 – mapping the periphery effect using a single object category (a) Examples of stimuli used in experiment 1. Line drawings of faces and buildings were shown either in the center of the visual field or in multiple enlarged copies in a peripheral ring. Subjects were instructed to fixate on a central dot. (b) Percent signal change measured in the CoS building-related region. A peripheral effect was obtained for both faces and buildings. (c) The same effect was obtained in the TOS building-related region. Asterisks denote a significant difference in a one-tailed t-test (*p<0.05, **p<0.005, ***p<0.001).

Experiment 2 – a single peripheral object

In experiment 1 the peripheral stimuli consisted of rings containing multiple objects. Therefore the peripheral effect may have been due to the increased number of objects in the periphery or to the ring-like arrangement typical of eccentricity-mapping stimuli. To explore these possibilities we conducted experiment 2.
In this experiment, we enlarged single building images shown in the center of the visual field (Fig. 3a, 'Central building') so that they impinged on the visual field periphery (Fig. 3a, 'Peripheral building'). The enlarged building images were identical in shape and features to the central ones (see materials and methods). In two additional conditions, subjects were presented with middle sized images of other buildings and faces (Fig. 3a, 'Medium building' and 'Medium face').

Figure 3: Experiment 2 – Mapping eccentricity using a single object stimulus
(a) Examples of stimuli used in experiment 2. Stimuli were line drawings of buildings shown either in the center ('central building') or enlarged to fill the periphery ('peripheral building'). Note that the peripheral stimuli were identical to the central ones and only differed in size. Line drawings of faces and buildings of an intermediate size were also shown ('medium face' and 'medium building'). Subjects performed a 1-back task, while maintaining central fixation. (b) Percent signal change measured in the CoS building-related region. As expected this region exhibited preferential activation to buildings compared to faces. Importantly, a peripheral effect was obtained even though the peripheral stimulus contained a single object. (c) A similar trend was observed in the TOS region. Asterisks denote a significant difference in a one-tailed t-test (*p<0.05, **p<0.01).
The results, averaged across five subjects, show that the periphery-effect in the CoS was preserved when the peripheral stimulus was a single enlarged building (Fig. 3b, peripheral building vs. central building, p<0.01, one-tailed t-test, n=5). As expected, this region also exhibited preferential activation to buildings compared to faces (medium building vs. medium face, p<0.05). The activation to these "middle sized" buildings was in between the activation to the central and peripheral buildings (central building: 0.24%±0.06% mean ± SEM, medium building: 0.45±0.06%, peripheral building: 0.75±0.09%). A similar peripheral bias was observed in the TOS, (Fig. 3c, peripheral building vs. central building, p<0.01, n=5). Thus, we conclude that the periphery-effect was not due to a difference in the shape or number of object stimuli presented.

Experiment 3 – effect of peripheral location versus large area of stimulation

The results of experiment 2 were also compatible with the possibility that the peripheral effect was due to the larger area covered by the peripheral stimuli, rather than their peripheral visual field location. In early visual areas the visual field is represented in a log-polar manner, i.e. the representation of the center of the field is magnified compared to its periphery. Standard eccentricity mapping experiments compensate for the lower magnification factor in the periphery by enlarging the peripheral stimuli. The same manipulation was used in experiments 1 and 2. However, it is important to note that this experimental design confounds peripheral location with a larger stimulation area. It could be that the peripheral effect observed in the CoS is in fact a result of the larger area occupied by the peripheral stimuli compared to the mid or central ones.

To explore this possibility we conducted experiment 3. The experiment enabled us to perform two comparisons. First, we could compare activation to stimuli which differed both in their eccentricity and in the extent of area they covered, similar to previous experiments (Fig. 4 top). We term this
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mapping 'logarithmic eccentricity'. In addition, we could compare activation to stimuli which had equal stimulation areas but differed in their maximal eccentricity (Fig. 4 bottom). We term this mapping 'Euclidean eccentricity'. If the peripheral effect was due exclusively to the larger overall stimulated area covered by the peripheral stimuli, then we would expect similar activation levels to stimuli presented in different locations, provided that their areas were identical. In each condition separate epochs contained either building or object images, but since there was no significant difference in the percent signal change between these conditions (two-way ANOVA, main factors: category and location; interaction, CoS: p=0.9; TOS: p=0.88), we averaged the results across category.

Figure 4: Experiment 3 – "Euclidean" vs. "logarithmic" eccentricity mapping
Examples of stimuli used in experiment 3. Stimuli were drawings of buildings and objects shown in four different locations. 'Logarithmic periphery' and 'logarithmic mid' stimuli were used to map the peripheral effect similar to previous experiments ('logarithmic eccentricity'). Equal sized 'Euclidean periphery' and 'Euclidean mid' stimuli were used to measure the net peripheral effect due to peripheral location and not to stimulus size ('Euclidean eccentricity'). Subjects were instructed to fixate a central dot.

Fig. 5 shows the average eccentricity maps obtained in a group of eight subjects. The top map was created by contrasting activation to the small mid-eccentricity ring with activation to the magnified peripheral one ("logarithmic eccentricity"), as was done in previous experiments. The bottom map was created by contrasting activation to the equal-sized mid and periphery rings ("Euclidean eccentricity").
Results 31 eccentricity”). Superimposed on the maps are the contours of building-related activations in the localizer experiment averaged across the same subjects.

Figure 5: "Euclidean" vs. "logarithmic" eccentricity mapping: activation maps
The periphery effect was obtained using stimuli which were magnified compared to the more central stimuli (top) and also using stimuli which were equal in size (bottom). Note that most of the CoS building-related region (yellow contours) was within the periphery-biased area, except for the most anterior tip. Color scales indicate the significance of the statistical test. Abbreviations as in Fig. 1.
Importantly, in posterior low-tier areas a clear center-periphery map was obtained in both comparisons, indicating that subjects indeed maintained fixation. As expected, in these areas, equating the size of the stimuli enlarged the cortical area responding to the mid stimuli and reduced the area responding to the peripheral ones. Also as expected, most of the CoS building-related region (yellow contours) was preferentially activated by the peripheral stimuli when the periphery was enlarged compared to the mid-stimulation. However, critically, the same peripheral bias was observed even when the total areas of the mid and peripheral stimuli were equated.

Sampling the building-related regions yielded a periphery-effect both in the CoS and in the TOS when the peripheral stimuli were magnified ("Logarithmic eccentricity", periphery vs. mid, CoS: p<0.05, n=8; TOS: p<0.05, n=5). Comparison of activation to stimuli which differed only in their location revealed a trend toward the periphery which was close to significance in the CoS ("Euclidean eccentricity", periphery vs. mid, p=0.08, n=8) but not in the TOS (p=0.12, n=5). Previously (Levy et al., 2001) we have reported that the most anterior tip of the building-related region may be outside of the periphery-biased area. In order to avoid mixing such non-peripheral regions, we conducted another analysis, in which only voxels showing the conventional ("logarithmic") periphery-effect, which lay anteriorly to retinotopic areas in the CoS and TOS were examined (Fig. 6). Our results show that these voxels manifested a significant bias towards the visual field periphery even when stimuli were equated in their stimulated area, both in the CoS (periphery vs. mid, p<0.0005, one-tailed t-test, n=6) and in the TOS (p<0.05, n=5). Thus, it seems that the periphery effect in the CoS was largely due to the peripheral location of the stimuli. However, this does not rule out an additional area effect. To test for such an effect we sampled the data again, this time localizing voxels showing either a logarithmic or a Euclidean periphery bias (logarithmic periphery + Euclidean periphery vs. logarithmic mid + Euclidean mid). This enabled us
to compare activation to the logarithmic vs. Euclidean periphery conditions, which were identical in their extreme eccentricity but differed in the area they covered. The comparison revealed a significantly higher activation to the logarithmic periphery ($p<0.05$, one-tailed t-test, $n=6$) in the CoS and a similar, albeit not significant, trend in the TOS ($p=0.1$, one-tailed t-test, $n=5$). Thus, an area effect seems to exist in building-related areas, in addition to the true periphery effect.

Figure 6: "Euclidean" eccentricity mapping: time course analysis
Percent signal change in response to the equal-size stimuli, measured in voxels which exhibited a bias toward the enlarged periphery in the CoS (a) and the TOS (b) anteriorly to retinotopic areas. The peripheral effect in these voxels was preserved even though the area covered by the stimuli was equated. Asterisks denote a significant difference in a one-tailed t-test (*$p<0.05$, **$p<0.0005$).
Discussion

The nature of the peripheral effect in the CoS

The results of experiment 1 show that the periphery effect of the CoS was not specific to stimuli which preferentially activated the CoS, such as buildings, but could be obtained even using faces, which hardly activated this region when presented centrally. A likely explanation for this result appears to be the marked reduction in category-selectivity for peripheral stimuli observed in the CoS. Thus, the CoS showed a higher selectivity to building images when these images were presented centrally compared to when they were presented peripherally, although in terms of overall activation, the peripheral stimuli produced a higher activation level. It is not clear what the source of this differential selectivity is. One possibility may be an interaction with the neighboring Fusiform gyrus, so that the high activation to faces presented centrally in this region, is causing, via some sort of "lateral inhibition" process, the reduction in face activation in the CoS. However, additional tests will be required to clarify the mechanisms underlying this finding.

Experiment 2 ruled out the possibility that the periphery effect was due to the number of objects presented or the ring shape of the conventional peripheral stimulus. In this experiment, unlike conventional eccentricity mapping experiments, the peripheral stimuli were constructed by enlarging a single central object. In terms of shape, the central and peripheral stimuli shared the exact same features and differed only in their size, yet, the periphery effect was maintained. These results are compatible with a previous study (Epstein and Kanwisher, 1998), which failed to find preferential activation to multiple objects compared to a single object in the PPA, unless these objects were arranged in a spatial context.
It should be noted that the result of Experiment 2 cannot be interpreted as produced by a sharply localized retinotopic effect, similar to early visual areas, since the increase in activation when moving from central building stimuli to the middle sized ones and then to peripheral ones was gradual (Fig. 3b). Thus, a clear-cut outcome of experiment 2 is the finding of a gradual size effect in the CoS, by which larger objects produced higher activation than smaller ones.

However, the size effect in the CoS in this experiment might be due either to the stimuli impinging on more peripheral visual field locations, or purely due to the larger area of the visual stimuli. Experiment 3 was designed to differentiate between these two alternatives, and its results indicate that a large fraction of the effect, at least for mid to peripheral locations, was a true peripheral bias. Thus, even when the area of stimulation was equated, stimuli in more peripheral locations still caused a preferential activation (Fig. 6). This could mean that a single object in some part of the peripheral visual field is enough to activate the CoS. However, the results of a recent study (Epstein et al., 2003) show that, at least in the PPA, this is not the case: two small objects in the periphery did not activate this region more than a single object in the center. In addition, we found that enlarging the area of the stimulus also increased the activation in the region. Thus it seems that visual stimulation occupying a large part of the visual field and spanning a wide range of polar angles is needed in order to activate the region. The results of experiment 3 also provide further confirmation to the finding that the number of objects included in the stimuli was not critical for activation, since in both the peripheral and the mid stimuli there was an identical number of objects (Fig. 4 bottom).

Note that the results could not be explained by differential eye-movement patterns, since clear center-periphery maps were obtained in early retinotopic areas (e.g. see Fig. 5 for experiment 3.)
Similar maps were obtained in experiments 1 and 2). Such clearly demarcated eccentricity maps provide an intrinsic control which indicates that subjects did not deviate from fixation, since due to the high foveal magnification such deviations would have resulted in a substantial blurring of the boundaries of the foveal/peripheral representations.

**Implications for the center-periphery organization**

How are the present results related to the center-periphery organization? Several lines of evidence suggest that qualitatively different processes take place in the center-biased pFs and the periphery-biased CoS and PPA. A number of studies have implicated the pFs in object recognition. Whether it contains a module, specialized for face recognition (Kanwisher, 2000) or an area of expertise, which can be trained to specialize in other objects (Gauthier et al., 2000), it appears that the pFs singles out for detailed analyses specific objects of interest embedded in the visual scene. This is compatible with the center-bias found in this region, which implies higher resolution compared to the CoS. This high resolution enables a fine analysis of the visual information, leading to extraction of objects or features matching some templates which are represented in this region. This is not to say that the pFs deals primarily with local features. On the contrary, several studies have shown that the response of this region is more holistic than feature-based (e.g. (Hasson et al., 2001; Kourtzi and Kanwisher, 2001). The PPA, on the other hand, was shown to deal with the overall layout of the visual environment. Thus, it was highly activated by outdoor scenes, even more than by buildings (Epstein and Kanwisher, 1998) and it seems to be sensitive to the spatial arrangement of the visual stimuli and to its inter-relationship. For example, the PPA was more activated by intact room images compared to images which were fractured and rearranged, and by scenes containing no objects compared to objects with no spatial context (Epstein and Kanwisher, 1998). This notion of sensitivity to global spatial arrangement was emphasized by the recent finding that the
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representation in the PPA is viewpoint-specific (Epstein et al., 2003), i.e. sensitive to changes in the spatial relationship between the scene and the observer.

The peripheral effect found in the CoS is compatible with a role in navigation and representation of the visual environment. Navigation entails integration and comparison of information across the visual field and the present results are congruent with such long-distance “comparator” processes. Thus, activation in the CoS increased as the stimulus became more peripheral, even if the area it covered remained the same, and it also increased when the stimulus was enlarged, even if it did not reach farther eccentricities (Experiment 3). In addition, the peripheral effect did not depend on multiplicity of objects, but was associated with any kind of complex visual information (Experiment 2). It seems that the maximal eccentricity of the stimulus determines the level of activation in the CoS, which makes sense if comparison of information across large distances in the visual field is required. However, the fact that the periphery-effect remained for faces as well may imply that the CoS has a more general role in spatial integration. This role may be required for navigation but can also be used in other tasks. It should be noted that the region in the CoS which was the basis of analysis in these studies may not be identical to the PPA described by Epstein and Kanwisher. It could be that scene images activate a slightly more medial region compared to building images, and that this medial region is less responsive to other objects, even when presented in the peripheral field.

Further support for the notion that spatial integration is highly emphasized in peripheral stimuli comes from a recent study which explored the phenomenon of reduced acuity caused by clutter of stimuli in the periphery, known as 'crowding' (Parkes et al., 2001). This study demonstrated that even when clutter of stimuli in the periphery prevented subjects from estimating the orientation of
individual stimuli, they could still estimate the average orientation precisely, proving that they had access to information which was integrated across the field.

The difference between the pFs and the CoS does not necessarily imply the existence of segregated modules. It is compatible both with a modular organization (Spiridon and Kanwisher, 2002) and with a distributed one (Haxby et al., 2001; Avidan et al., 2002). The pFs and the CoS could either be two distinct entities performing different processes or two extremes of one continuum which starts with high resolution and fine analysis and ends with low resolution and global synthesis.

**The periphery effect in Dorsal occipito-temporal cortex**

The ventral building-related region in the CoS is mirrored by a dorsal region in the vicinity of the TOS which shows preferential activation to buildings compared to faces and common objects (Hasson et al., 2003). However, it is still not clear how these areas differ functionally. The preference for buildings does not necessarily mean that the region is *selective* to buildings. It could be that this region shows preferential activation to additional object categories, or that alternatively, both the CoS and the TOS regions are selective to buildings, but each performs a different process. Thus, for example, it could be that TOS is an intermediate region between the ventral stream, whose activation is related to stimulus appearance, and the dorsal stream, which deals with stimulus position (Aguirre and D'Esposito, 1997). Further research will be needed to define the properties of this region more precisely.
Methods

MRI Setup

Subjects were scanned on a 1.5T Signa Horizon LX 8.25 GE scanner equipped with a quadrature surface coil (Nova Medical Inc., Wakefield, Massachusetts), which covered the posterior brain regions. Blood oxygenation level dependent (BOLD) contrast was obtained with gradient-echo echo-planar imaging (EPI) sequence (TR = 3000ms, TE = 55ms, flip angle = 90°, field of view 24 × 24 cm², matrix size 80 × 80). The scanned volume included 17 nearly-axial slices of 4 mm thickness and 1 mm gap. A whole brain spoiled gradient (SPGR) sequence was acquired on each subject to allow accurate cortical segmentation, reconstruction and volume-based statistical analysis. T1-weighted high resolution (1.1x1.1 mm) anatomical images of the same orientation as the EPI slices were also acquired to facilitate incorporating the functional data into the 3D space.

Subjects

21 subjects participated in one or more of the experiments (13 women, ages 20-52). Data of one subject were discarded due to problems in data acquisition and data of another subject were discarded due to excessive head motion. Of the remaining 19 subjects, 11 participated in Experiment 1, five in Experiment 2 and eight in Experiment 3. Of these, one subject participated in all three experiments, three participated in two experiments, and the rest in a single experiment. Building-related areas were localized in a separate experiment in 17 subjects and borders of retinotopic areas were delineated in 15 of those subjects. All subjects had normal or corrected-to-normal vision and provided written informed consent. The Tel-Aviv Sourasky Medical Center approved the experimental protocol.
Stimuli

Stimuli were generated on a PC, projected via an LCD projector (Epson MP 7200) onto a tangent screen positioned over the subject’s forehead, and viewed through a tilted mirror.

Experimental design

All three experiments started with a blank period of 21 sec and ended with a 15 sec blank period, during which a uniform gray screen and a fixation point were presented. The experiments were short-block designed. Each block lasted 9 sec and consisted of 9 images of the same type. Blocks were pseudo-randomly ordered and interleaved with 6 sec blank periods.

Experiment-1

This experiment was aimed at testing whether the periphery effect is object-selective. The experiment consisted of six conditions: 3 categories x 2 eccentricities. Black and white line drawings of faces and buildings as well as character strings (reported elsewhere (Hasson et al., 2002)) were shown either in the center of the visual field (diameter: 3°) or in a peripheral ring (inner diameter: 11.5°, outer diameter: 20°), which contained eight enlarged copies of the same stimulus. 16 different images of each type were used. Each image was presented for 200 ms, followed by an 800 ms blank. Each condition was repeated 4 times, except for the character conditions which were repeated 8 times each. Subjects were instructed to fixate on a red dot positioned at the center of the screen throughout the experiment.

Experiment-2

This experiment was aimed at distinguishing between the effects of peripheral location and multiplicity of objects. The experiment consisted of four conditions. Two conditions consisted of black and white line drawings of buildings, shown either in a small ring at the center of the visual field (inner diameter: 0.8°, outer diameter: 3.3°, ‘central building’) or enlarged to fill a peripheral
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region (inner diameter: 5°, outer diameter: 20°, 'peripheral building'). Note that the stimuli in the 'peripheral building' condition were identical to those in the 'central building' condition, except for their size, including a blank hole in the center of all stimuli (Fig. 3a). Two additional conditions contained black and white line drawings of faces ('medium face') and buildings ('medium building'), subtending 12° × 12°. In the 'central building' and 'peripheral building' conditions 72 different images of each type were used. In the 'medium face' and 'medium building' conditions 27 different images of each type were used. Each image was presented for 250 ms, followed by a 750 ms blank. The first two conditions were repeated eight times, and the last two conditions were repeated six times. Subjects covertly performed a sequential matching task (1-back) while fixating on a red dot presented throughout the experiment.

Experiment-3

This experiment was aimed at differentiating between the effects of the peripheral location of the stimulus and the visual field it covers. The experiment consisted of eight conditions: 2 categories x 4 combinations of eccentricity and size. Multiple copies of gray-level drawings of buildings and man-made objects (tools, cars and chairs) were shown in a ring in one of four sizes / eccentricities (Fig. 4): ten copies in a ring whose diameters were 2.5° - 8° ('Logarithmic mid'), ten enlarged copies in a ring whose diameters were 8° - 20° ('Logarithmic periphery'), 20 copies in a ring whose diameters were 2.5° - 14° ('Euclidean mid'), and 20 copies of the same size in a ring whose diameters were 14° - 20° ('Euclidean periphery'). Thus, we could compare activation to stimuli which differed both in eccentricity and in area ('logarithmic periphery' vs. 'logarithmic mid') or to stimuli which differed in eccentricity but covered a similar area ('Euclidean periphery' vs. 'Euclidean mid'). 18 different images of each type were used. Each image was presented for 200 ms, followed by an 800 ms blank. The first visual epoch in the experiments consisted of geometrical patterns.
and was modeled as a separate predictor in the statistical analysis. Subjects were instructed to fixate on a red dot presented throughout the experiment.

**Building Localizer**

Building-related regions were localized using an external block-designed localizer (Hasson et al., 2003). Subjects were presented with images of buildings and faces (and two other conditions: common objects and patterns not used here). Each condition lasted 9 sec and was repeated four times (one subject), seven times (15 subjects) or eight times (one subject). The images were presented for a short duration (150-800ms), followed by a blank period. Epochs were pseudo-randomly ordered and interleaved with 6 sec blanks. Subjects had to covertly perform a 1-back task (16 subjects) or a recognition task (one subject) while fixating on a red dot.

**Mapping borders of visual areas**

The representations of vertical and horizontal visual field meridians were mapped in 15 subjects in order to delineate borders of retinotopic areas (Engel et al., 1994; Sereno et al., 1995; DeYoe et al., 1996). Stimuli were presented in 18 sec blocks, interleaved with 6 sec blank periods. Images were presented for 250 ms in a consecutive manner. Stimuli consisted of triangular wedges that were presented either vertically (upper or lower vertical meridians) or horizontally (left or right horizontal meridians). Each condition was repeated four times. Two versions of the experiment were run. In the first, the wedges consisted of either gray-level natural images or black and white objects-from-texture pictures (Grill-Spector et al., 1998). In the second, the wedges consisted of colored copies of objects superimposed on colored textures. Subjects were instructed to fixate on a small central cross.
**Data analysis**

fMRI data were analyzed with the BrainVoyager software package (R. Goebel, Brain Innovation, Masstricht, Netherlands) and with complementary in-house software. The first three images of each functional scan were discarded. The functional images were superimposed on 2D anatomical images and incorporated into the 3D data sets through trilinear interpolation. The complete data set was transformed into Talairach space (Talairach and Tournoux, 1988). Preprocessing of functional scans included 3D motion correction and filtering out of low frequencies up to 5 cycles per experiment in Experiment 2 and 10 cycles per experiment in all other experiments. No spatial smoothing was applied to the data. The cortical surface was reconstructed from the 3D-SPGR scan. The procedure included segmentation of the white matter using a grow-region function, the smooth covering of a sphere around the segmented region, and the expansion of the reconstructed white matter into the gray matter. The surface was then unfolded, cut along the calcarine sulcus and flattened. Statistical analysis was conducted on the flattened cortex.

**Statistical Analysis**

Building-related regions were identified in each subject using the building localizer experiment. Statistical analysis was based on the General Linear Model (Friston et al., 1995). A box-car predictor, assuming a 3 sec hemodynamic lag, was constructed for each experimental condition except blank, and the model was independently fitted to the signal of each voxel. A coefficient was calculated for each predictor using a least-squares algorithm. A t-test contrasting the coefficient of the building predictor with that of the face predictor was conducted, and regions of interest (ROI's) were defined as clusters of at least 6 contiguous functional voxels in which the p value of the test was less than 0.05 and which lay anteriorly to the retinotopic areas. In two subjects for which we did not map the retinotopic borders the ROI's were defined as the most anterior part of the
activated area (starting at 4cm from the posterior edge of the flattened hemisphere in the CoS and 3cm in the vicinity of the TOS).

In experiments 1-3 we sampled the time-course in each ROI and computed the percent signal change compared to the blank period preceding it. Repetitions of each condition and all the time points in each condition were then averaged. Finally, results were averaged across subjects.

In experiment 3 additional ROI's were defined as regions showing a periphery effect in the CoS and the TOS, by contrasting the predictors of the 'logarithmic periphery' and the 'logarithmic mid' conditions (Fig. 4). The time course of the 'Euclidean periphery' and 'Euclidean mid' conditions, which were not included in the statistical test was sampled and averaged as explained above.

**Periphery-bias index**

In experiment 1 a periphery bias was calculated for each object category in each ROI of each subject. The periphery bias was defined as:

\[
\frac{\text{periphery-center}}{\text{periphery+center}}
\]

where periphery and center are the percent signal changes compared to blank in the periphery and center respectively averaged across the time points in each epoch and the repetitions of each condition. A periphery-bias of 1 reflects a total preference for the peripheral visual field, whereas a value of 0 reflects equal activation to the central and peripheral visual fields.

**Multi subject analysis**

In the multi-subject analysis time courses of all subjects were converted into Talairach space and z-normalized. The multi-subject maps (Fig. 5) were obtained using a random effect procedure (Friston et al., 1999) and the maps were projected on a flattened Talairach normalized brain.

**Statistical significance**

Calculation of significance values in the activation maps (Figs. 1,5) was based on the individual voxel significance and on the minimum cluster size of 6 voxels (Forman et al., 1995). The
probability of a false positive was determined from the frequency count of cluster sizes within the entire cortical surface, using a Monte Carlo simulation (AlphaSim by B. Douglas Ward, a software module in Cox, 1996).

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References


2.3
Sub-structure of the human posterior fusiform gyrus
Abstract

It is an ongoing debate whether the complex activation patterns to different objects in the human ventral occipito-temporal cortex (VOT) reflect a modular representation of objects or a distributed one. Here we provide evidence for a third alternative: a smooth, orderly, topography. Specifically, using head images in front and back views we obtained activations of highly overlapping yet slightly offset regions in the fusiform gyrus. Crucially, the direction of this displacement was consistent across subjects and therefore cannot be attributed to random variability. This activation pattern reflects a continuous topography, in which representations of related objects "slide" smoothly along the fusiform gyrus.

Introduction

Neuroimaging studies of the human occipito-temporal cortex have revealed a complex organization of functional specializations in the cortical activation patterns in response to presentation of different object images. Two opposing views have been suggested in an attempt to interpret these specializations. On the one hand, a modular perspective has proposed that certain object categories, such as faces and places, constitute independent anatomical cortical modules specialized in processing of specific object categories (e.g. (Kanwisher et al., 1997; Aguirre et al., 1998; Epstein and Kanwisher, 1998)). On the other hand, an alternative view argued for a fully distributed system, in which the entire ventral occipito-temporal cortex is involved in representing various objects (Haxby et al., 2001). We have recently proposed a scheme that is somewhat in between these two extreme views, in which ventral occipito temporal (VOT) cortex is organized in an orderly topography, based on the arrangement of eccentricity-biases (Levy et al., 2001; Hasson
et al., 2002; Malach et al., 2002). We hypothesized that such eccentricity-biases allow optimal allocation of magnification factor, i.e. resolution resources, to different recognition processes.

An orderly topographic map of eccentricity, such as the one found in early retinotopic cortex, is typically a smoothly changing entity. However, the high order eccentricity map found in ventral stream areas is substantially different compared to early retinotopy on several grounds. First, the retinotopic selectivity is greatly reduced, so that only when activations to similar object shapes are compared at different visual field locations, can the eccentricity biases be revealed. Second, the cortical magnification factor undergoes substantial changes in high order areas. In particular, the mid-periphery representation appears to be substantially shrunk (Levy et al., 2001) (see also (Tootell and Hadjikhani, 2001)). Thus, the currently available data does not rule out the possibility of a modular organization within occipito-temporal cortex, which is "super-imposed" on an eccentricity-biased map.

In a modular organization, a discrete cortical area is activated by certain stimulus types (e.g. certain object categories, certain shape features etc.) and not by others. Each module is bounded and separate from other modules (Fig. 1a). Say we know that an area is activated by a certain stimulus type, “a” (red box in Fig. 1a). Using another stimulus type, “b”, we will expect one of three possibilities: 1. “b” will activate the same area. 2. “b” will avoid this area and activate a different area (e.g. the blue box in Fig. 1a). 3. “b” will activate both this area and other areas. Basically, this is a binary, “all or none” situation, in which each stimulus type will either activate the putative module or not.
Figure 1: Modular vs. continuous representation of objects in VOT

Two possible models for the representation of objects in area VOT.

(a) Modular representation – the object-related cortex consists of discrete entities, having sharp boundaries. If a certain stimulus type activates a certain area (e.g. front faces, red box) then other types of stimuli (e.g. back of the head images) will either activate this area as well (possibly in addition to other areas), or avoid this area and activate a separate area (e.g. the blue box). Other stimulus types will activate other separate locations (gray boxes). Note that in this case, the distance between centers of activation patches (white arrow) is at least equal to the patch size (black arrow).

(b) Continuous representation – activation (depicted by the height of the 3D shape) to different objects "slides" smoothly along the continuous map. The activation to front and back images (red and blue) will be partly overlapping and partly offset. Open arrows point to non-overlapping areas. Note that here the distance between centers of activation patches (white arrow) can be far smaller than the patch size (black arrow). No sharp modular borders are assumed in this organization.

An alternative organization is that of a graded topography (Fig. 1b). Here the prediction is that the representation of different types of stimuli will "slide" smoothly within the object-related cortex. In this case, "a" and "b" may activate partially overlapping areas which are slightly offset relative to each other (red and blue in Fig. 1b). Such slightly offset areas have specific geometrical
relationships that distinguish them from a modular organization (see Fig. 1). Specifically, the
distance between the centers of the activations for "a and b" should be less than the size of
activated region to either "a" or "b". Furthermore, there should be strips of non-overlapping
activations that should have consistent directional relationships to the overlapping zone (e.g. Fig.
1b - the red and blue non-overlapping strips).

In searching for appropriate images that might expose such fine-grain sub-structures, we opted to
examine the nature of the representation of objects in the fusiform face area (FFA (Kanwisher et
al., 1997)) by using the contrast between front and back views of head images. Previous work
(Tong et al., 2000) has shown that strictly within the FFA, back of the head images show
significantly reduced activation. From the perspective of eccentricity-related topography based on
resolution demands, this is reasonable, since recognition based on back of the head images
presumably depends more on global head contours and texture integration, and less on analysis of
fine detail, compared to recognition based on front-face images. On the other hand, both front and
back of the head images engage closely related recognition processes, which may provide a
sensitive test of the topographic "graininess" within the fusiform gyrus.

If the putative face-related area is indeed a discrete, modular, entity, then back images should
either activate this area as well, possibly in addition to other areas, or avoid this area completely
and activate separate areas (e.g. Fig. 1a). Alternatively, in the case of a smoothly graded
topography, we would expect the activations to front and back images to be partly overlapping and
partly offset relative to each other (Fig. 1b). In such a model activation to different objects "slides"
smoothly along the VOT, where different objects may activate partially overlapping regions,
depending on factors such as resolution needs.
Results

Our results show that back-of-the-head images activate the posterior fusiform gyrus in high overlap with the activation to front faces. Crucially, however, the two activation patterns were slightly but consistently offset relative to each other. The relative anatomical axis of displacement was consistent across all subjects and could not be attributed to random variability. These fine-grain displacements clearly indicate the existence of a smoothly graded functional topography within the human fusiform gyrus, at least within the resolution limits of conventional fMRI.

Results

To explore the nature of the Fusiform topographic organization we mapped the activation to head images in front and back views (Fig. 2a). Stimuli were constructed so that front images had higher spatial spectral energy than back images, both in the central and peripheral parts of the images. Thus constructed, higher activation to back images in any part of the brain cannot be attributed to higher energy. Stimuli were presented in short blocks of the same stimulus type, interleaved with blank periods (Fig. 2b), and subjects were instructed to perform a sequential matching task, while fixating on a central dot.

Figure 2: Front and back experiment
(a) Examples of stimuli used to map representations of front and back of the head images.
(b) A sample of the temporal sequence of image presentations in the experiment. Images were presented at 1 HZ, in short (9 sec) blocks, interleaved with (6 sec) blank periods (see methods for more details).
The peak of highest activation to each condition was located using the “single-condition” contrast (Hasson et al., 2002), i.e. searching for voxels which showed activation during each condition compared to blank (front vs. blank and back vs. blank). The advantage of such an approach over the more conventional “contrast” approach, i.e. comparing front vs. back activations, is that there is no a-priori assumption concerning the existence of areas showing preferential activation to one condition over the other.

Fig. 3 presents the results in the right hemisphere of a representative subject. The activated region includes retinotopic areas (posteriorly to the dotted line, see Methods) and extends anteriorly to the Ventral Occipito-Temporal cortex (VOT (Malach et al., 2002)). Both conditions activated the posterior fusiform gyrus (pFs), a region which is anterior to areas V4/V8 (Hadjikhani et al., 1998) and lateral to the collateral sulcus (CoS), extending into the occipito-temporal sulcus, and corresponds to the fusiform face area (FFA) described previously (Kanwisher et al., 1997). This face-related region was identified in a number of other studies (Clark et al., 1996; Puce et al., 1996; McCarthy et al., 1997; Halgren et al., 1999; Ishai et al., 1999). As depicted in the figure, the activations to front and back images were highly overlapping (purple in Fig. 3). Crucially, however, the activation maps for front and back images were slightly offset relative to each other, such that front images activated an additional narrow strip laterally, while back images activated an additional medial strip (red and blue respectively). It is important to emphasize that in this and subsequent analysis an identical statistical threshold was used for the back and front face conditions, so the offsets between these conditions cannot be attributed to differences in statistical thresholds.
Figure 3: Activation to front and back of the head images in VOT

An example of front and back related activation in the right hemisphere of one subject. The activated areas are presented on the inflated hemisphere. Inset shows enlargement of the activated area. The dotted line represents the anterior border of retinotopic areas. Anteriorly to it lies area VOT. The activation to front and back in VOT was highly overlapping (purple), yet slightly displaced, where front images activated a more lateral region (red) and back images activated a more medial region (blue). Building images activated an area in the CoS, more medial to the back images, which is shown for comparison (green). Arrows indicate areas of non-overlapping activation. VOT, Ventral Occipito-Temporal; pFs, posterior fusiform gyrus; CoS, collateral sulcus; Ant, Anterior; Post, Posterior; Lat, Lateral; Med, Medial
Activation to building images was also mapped in a separate experiment. Building images activated the medial part of VOT along the anterior part of the collateral sulcus (green), compatible with previous studies (Aguirre et al., 1998; Epstein and Kanwisher, 1998; Ishai et al., 1999; Levy et al., 2001). This building-related region was clearly separated from the region activated by back images and more medial to it. The activations to front, back and building images create a lateral-medial axis which is parallel to the axis of eccentricity biases previously found in these areas (Levy et al., 2001; Hasson et al., 2002).

A similar trend can be seen in a map averaged across 9 subjects (Fig. 4), both in the left and right hemispheres. Here too, the activation to front and back images was largely overlapping but slightly offset, such that back images activated an area slightly medial to the area activated by front images, yet separate from the building-related area and lateral to it.

In addition to the VOT, front and back images activated regions in the lateral occipital cortex (LO), which is situated posteriorly to area MT, in the vicinity of the lateral occipital sulcus and the posterior inferotemporal sulcus (Fig. 4). In 15 out of 18 hemispheres the activations were not completely overlapping. However, in contrast to VOT, there was no consistency in the anatomical relationship between the regions activated by the two conditions. In some cases the activation to back images appeared to be more anterior compared to the activation to front images, while in other cases the displacement was along the dorso-ventral axis, where back images activated either more ventral or more dorsal regions. Finally, in 17 out of 18 hemispheres front and back images also activated a region in the intraparietal sulcus (IPS, Fig. 4). This activation was usually much stronger to back images compared to front ones (15 of 17 hemispheres), and the statistical
threshold had to be decreased substantially in order to obtain comparable activation to front images.

![Multi-subject activation to front and back of the head images](image)

**Figure 4: Multi-subject activation to front and back of the head images**

Activation to front, back and building images averaged across 9 subjects, presented on the flattened hemispheres of one subject. Insets show enlargements of activated areas. Activation to front and back images was highly overlapping (purple), yet front images activated a slightly more lateral region (red) and back images activated a slightly more medial region (blue). Activation to buildings (green) was medial to the activation to back images and separate from it. Arrows indicate non-overlapping activation. LO, Lateral Occipital; IPS, Intra Parietal Sulcus. Other abbreviations as in fig. 3.
It could be argued that the activation to back images in VOT completely overlaps the front activation, and that the slight offset was a consequence of random fluctuations due to, e.g. head and respiratory motions. However, the displacement was always along the eccentricity axis, and inspection of the activation in VOT in individual subjects revealed that despite the small size of the anatomical displacement and large inter-subject variability, the neuro-anatomical direction of displacement was highly consistent: back images activated regions which were slightly more medial than front images. The average displacement between the peaks of highest activation to front and back images (1-2 voxels) was 5mm±3mm std in the right hemisphere and 4±2 mm in the left hemisphere (see Table 1 for Talairach coordinates). Given that the fMRI spatial resolution was 3mm, the proximity of peaks we obtained was just next to complete overlap. Figure 5 shows enlarged flattened maps of the representative subject from Fig. 2 (SN) and the right hemispheres of 3 additional subjects (HT,ZH and NL) showing the same pattern of activation (‘pattern a’). The fifth example, Subject BB, also exhibits this pattern in both hemispheres. However, this subject had an additional focus of back activation in the right hemisphere, which is medial to the front focus (‘pattern b’).

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Talairach (Talairach and Tournoux, 1988) coordinates of highest activation to front and back images. Values are mean ± s.d. in mm.
Figure 5: Inter-subject comparison of the activation to front and back of the head images.
Activation to front and back images on the flattened hemispheres of 5 subjects. Four right hemispheres (SN, HT, ZH and NL) exhibit ‘pattern a’ activation (see text for details). Two hemispheres of subject BB are presented. The right hemisphere exhibits ‘pattern b’, while the left hemisphere exhibits ‘pattern a’. Left hemisphere is presented in a right hemisphere orientation for comparison purposes. Arrows indicate non-overlapping activation. RH, Right Hemisphere; LH, Left Hemisphere. Colors and other abbreviations as in fig. 3.

All these cases are compatible with a scheme we will term “front=lateral”, according to which front faces activate a slightly more lateral, and therefore more foveal, area than back images.
Hypothetically, we can think of an opposite scheme, in which back images are the ones that activate more lateral representations – the “back=lateral” scheme. This scheme encompasses two organizations which mirror the ones in the “front=lateral” scheme: activation to front faces which is more medial to the activation to back images (‘pattern e’, Fig. 6), and the same pattern with an additional focus of activation to front faces, which is more lateral (‘pattern d’). For completion, we include the possibility that the back activation fully overlaps the front activation (‘pattern c’).

The statistical analysis (Fig. 6) shows that in 8 out of 9 right hemispheres the pattern of activation followed the “front=lateral” scheme (5 in pattern a and 3 in pattern b) and one hemisphere exhibited a full overlap. Importantly, none of the right hemispheres followed the “back=lateral” scheme. Note
that random variability should create a roughly equal number of “front=lateral” and “back=lateral” cases. In fact, all right hemispheres but one exhibited the “front=lateral” scheme (i.e. either pattern “a” or “b”), and none the “back=lateral” scheme. This result is highly significant statistically (Binomial test p<0.004 n=8). In the left hemisphere there was a similar trend, with only one hemisphere exhibiting the “back=lateral” pattern. However, 3 hemispheres showed complete overlap of activation to front and back images, and therefore the trend did not reach significance.

**Discussion**

**A graded topography**

The main finding reported here concerns the neuro-anatomical organization of the fusiform gyrus. The fact that front and back of the head images were mapped to largely overlapping, but consistently offset regions, is compatible with the notion that the fusiform gyrus contains a continuous, smoothly changing topography. It is interesting that analysis of the organization of intrinsic axonal and dendritic architecture in primate visual cortex, also leads to the conclusion that smooth transitions are the rule rather than the exception in cortical circuitry (Malach, 1994). Our results argue against the notion that this cortical tissue consists of anatomically segregated, sharply defined modules. A modular organization should be associated with more "binary" maps in which different object images are mapped either in complete overlap (in those cases where they belong to the same "module", or in a segregated manner (in those cases where they belong to different "modules"). The very slight offset (~1 voxel) revealed in the activation to front vs. back images (Fig. 5) can not be attributed to random variability, since its direction was consistent across subjects, hence it is not compatible with a modular organization. Rather, it suggests that there are
Results

no sharp modular boundaries, and each object can occupy a different territory within a smoothly graded topography.

Thus, of the two possible models for the human fusiform gyrus presented in Fig. 1, our results support the graded-topography model (Fig. 1b). Note that no sharp boundaries are proposed for this cortex; rather, our data supports a smoothly changing topography in which representations of objects may occupy different regions depending on factors such as resolution demands. It should be emphasized also that it is not clear at present how specific each cortical region is for a particular object category, and it may well be that each part of the topography is shared by object images of numerous categories (Haxby et al., 2001). Note also that at a finer resolution, the gradual topography could be broken up into a mosaic of shape-columns (Tanaka, 1996; Tsunoda et al., 2001).

Relevance to object modularity

While the strikingly consistent specialization for various object categories has been amply documented in human neuroimaging (Puce et al., 1996; Kanwisher et al., 1997; Aguirre et al., 1998; Epstein and Kanwisher, 1998; Chao et al., 1999; Gauthier et al., 2000; Downing et al., 2001), the degree of this modularity and its significance has been a central topic of debate (e.g. (Kanwisher, 2000; Haxby et al., 2001)). Our results showing a graded topography support a scheme which is somewhat in between a strictly modular view, consisting of functionally uniform object selective neurons, and a fully distributed network. Such an intermediate modularity is in fact evident in the functional profiles obtained in object-selective areas, which invariably show a significant activation to "non-optimal" object categories (Kanwisher et al., 1997; Ishai et al., 1999; Chao et al., 2002; Hasson et al., 2002). Recently our group has obtained evidence suggesting that
the sub-optimal object activation may reflect the existence of small neuronal groups, which are actually selective for these "non-optimal" objects (Avidan et al., 2002). This view of a biased, yet heterogeneous, object-selective mosaic is also compatible with findings in macaque monkeys in which face-columns interdigitate with neighboring columns sensitive to non-face stimuli (Tanaka, 1996; Tsunoda et al., 2001).

**Eccentricity and object-related activation**

Our results are compatible with the hypothesis that the arrangement of different objects within the VOT is biased by acuity demands (Levy et al., 2001; Hasson et al., 2002; Malach et al., 2002), so that objects such as front faces, whose recognition entails analysis of fine detail (e.g. facial features, facial expressions) will be biased towards more foveal vision. From this perspective, recognition through back of the head images, is dependent on the overall head contour which may require somewhat less fine detail analysis, and consequently will be displaced more medially relative to front faces. However, the exact topographic principle that underlies the observed activation shift is not clear at present, so other interpretations for the medial displacement, such as different shape features, cannot be ruled out.

**The lateral "back" focus**

In 4 out of 13 hemispheres which exhibited the "front=lateral" pattern, we observed a second activation by back of the head images, situated laterally to the front face activation. A parsimonious interpretation of this result is that, as in early retinotopy, the VOT foveal-biased representation is "sandwiched" between two mid-periphery biased regions, so moving away from foveal bias translates occasionally to splitting the representation into two foci. Alternatively, it could
be that the front face representation corresponds to the most lateral part of the VOT, and the additional focus belongs to a second entity - perhaps even the most anterior-ventral part of LO.

**Activation to back of the head images in other cortical regions**

Apart from the VOT, front and back images also activated regions in the vicinity of LO and a locus in the IPS. In most subjects the activation to front and back images in LO was partly overlapping, but largely separate. The region activated by back images may correspond to the body-part area (EBA (Downing et al., 2001)). However, we failed to find a consistent relationship between the anatomical location of front and back activation in different subjects. The underlying causes of such displacements are not clear and might relate to the many other dimensions that differentiate back and front of the head images. Thus, for example, back images consist mainly of hair, which typically contains a texture of elongated lines, whereas front images contain several separate distinct features.

In the IPS, activation was much stronger to back images than to front ones. It is tempting to speculate that the strong back activation here may be a result of an involuntary mental rotation process induced by the back of the head images (Gauthier et al., 2002).

**Differences between right and left hemispheres**

Although the same trend of results was found in both hemispheres, it was stronger in the right hemisphere. Three out of 9 subjects showed complete overlap of activation to front and back images in the left hemisphere, whereas only one subject showed such an overlap in the right hemisphere. This is compatible with the claim that the face-selective area is more pronounced in the right hemisphere (Kanwisher et al., 1997; Hasson et al., 2002).
Interestingly, a recent study found adaptation to objects presented in different viewpoints in the left fusiform and not in the right fusiform, suggesting that the left fusiform may generalize over different viewpoints while the right one does not (Vuilleumier et al., 2002). This effect may also explain the larger overlap we found between front and back image activations in the left hemisphere.

In monkeys, a continuous mapping of different face views has been found in IT, using optical imaging (Wang et al., 1998). The different views activated highly overlapping, yet slightly displaced locations. The location of activation shifted gradually in one direction with the rotation of the face. However, it should be emphasized that these effects were found on a much finer, columnar scale, compared to the present findings.

**Methods**

**Subjects**

Nine healthy subjects (2 women, ages 25-50) participated in the 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 acquisition**

Subjects were scanned on a 1.5 Signa Horizon LX 8.25 GE scanner equipped with a quadrature surface coil (Nova Medical Inc., Wakefield, Massachusetts), which covered the posterior brain regions. 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 $24 \times 24$ cm$^2$, matrix size $80 \times 80$). The scanned volume included 17 nearly-axial slices of 4 mm thickness.
and 1 mm gap. T1-weighted high resolution (1X1X1 mm) anatomical images were acquired and a 3D SPGR sequence was acquired on each subject to allow accurate cortical segmentation and reconstruction and volume-based statistical analysis.

**Visual stimuli**

Stimuli were generated on a PC and projected via an LCD projector (Epson MP 7200) onto a tangent screen positioned over the subject’s forehead, and viewed through a tilted mirror. A specially designed directional filter (3M Light Control Film) eliminated off axis viewing of the screen.

**Experimental protocol.**

Two versions of the experiment were run. The first version (4 subjects) contained 2 conditions: front and back. Stimuli consisted of gray level photographs of unfamiliar men and women in back and front views (Fig. 2), subtending 8 X 6.4 deg. Photographs were cropped so that the total spatial spectral energy in the front view was higher than in the back view both in the central and peripheral parts of the images (Levy et al., 2001). Stimuli were presented in 9 sec blocks interleaved with 6 sec blank periods, except for the first and last blank, which lasted 21 and 15 sec respectively. Each condition was repeated 14 times during the experiment. Each stimulus was presented for 300 ms, followed by a 700 ms blank. 63 different stimuli were used in each condition, and each was repeated twice during the experiment. The first epoch in the experiment consisted of pattern images and lasted 9 sec. A red central dot was present throughout the experiment and subjects were instructed to fixate on it and to covertly perform a sequential matching task (1-back). One or two stimuli were repeated in each block. The second version of the experiment (5 subjects) included an additional condition, not considered in the results reported here, in which front faces were enlarged and cropped to fit an equal ellipse. Each condition was repeated 10 times using 45
different stimuli. Subjects performed a 1-back task either covertly (2 subjects) or via a response box (3 subjects). Other details as in the first version.

**Localizing building-related areas**

Building-related areas were mapped using either line drawings (5 subjects) or gray-level photographs of buildings. Details can be found in (Avidan et al., 2002; Avidan et al., 2003).

**Mapping borders of visual areas**

The representations of vertical and horizontal visual field meridians were mapped in 5 subjects in order to delineate borders of retinotopic areas (Engel et al., 1994; Sereno et al., 1995; DeYoe et al., 1996; Grill-Spector et al., 1998; Grill-Spector et al., 2000). The dotted line in Fig. 3 is the anterior border of areas V4/V8. For details see (Levy et al., 2001).

**Data analysis**

fMRI data were analyzed with the BrainVoyager 4.6 software package (R. Goebel, Brain Innovation, Masstricht, Netherlands) and with complementary in-house software. The data of each subject from each scan were analyzed both separately and in a multi-subject analysis. The first three images of each functional scan were discarded. The functional images were superimposed on 2D anatomical images and incorporated into the 3D data sets through trilinear interpolation. The complete data set was transformed into Talairach (Talairach and Tournoux, 1988) space. Preprocessing of functional scans included 3D motion correction and high frequency temporal filtering. Statistical analysis was based on the General Linear Model (Friston et al., 1995). A box-car predictor, assuming a 3 sec hemodynamic lag, was constructed for each condition except blank, and the model was independently fitted to the signal in each voxel. To locate areas of highest activation to each condition, the model was fitted again, each time excluding one predictor, and the contribution of each predictor to the explained variance was thus computed.
The cortical surface was reconstructed from the 3D-SPGR scan. The procedure included segmentation of the white matter using a grow-region function, the smooth covering of a sphere around the segmented region, and the expansion of the reconstructed white matter into the gray matter. The surface was then unfolded, cut along the calcarine sulcus and flattened. The obtained activation maps were superimposed on the unfolded cortex.

Multi-subject analysis (Fig. 4): the time-courses of all subjects were transformed into talairach space, z-normalized and concatenated, and the statistical tests were performed on the concatenated time course. The results are presented on the flattened hemispheres of one subject.

Non-parametric statistics (Fig. 6): the frequency of the two possible cortical schemes (‘front=lateral’ and ‘back=lateral’) was computed. Under random conditions, the probability of each scheme is 0.5. The probability of the obtained results is therefore:

\[
p = \binom{x}{n} 0.5^x \cdot 0.5^{n-x}
\]

where \(p\) is the total probability, \(n\) is the total number of hemispheres showing both possible displacement schemes and \(x\) is the hemispheres exhibiting the ‘front=lateral’ scheme.
References


2.4
One picture is worth a million neurons
The nature of object representation in the human brain is a matter of great debate. In particular, the number of neurons participating in the representation of a single object varies substantially in different theoretical models. Here we used fMRI to obtain a lower bound estimate of this number. Measurements of V1 activations were used to “calibrate” the estimates of occipito-temporal cortex activations. Our results show that at least a million neurons in object-related cortex, and about two hundred million neurons in the entire visual cortex, are involved in the representation of a single object image.

How many neurons participate in the representation of a single visual image? The answer to this straightforward question is critical for constraining biologically inspired models of object recognition, which vary greatly in their assumptions - from very few "grandmother cells" (Konorski, 1967) to numerous neurons in widely distributed networks (Shadlen and Newsome, 1998).

In recent years, the introduction of functional imaging techniques such as fMRI, provides an opportunity to explore this issue. Several studies (Boynton et al., 1996; Heeger et al., 2000; Rees et al., 2000; Logothetis et al., 2001) have shown that fMRI BOLD signal is proportional to neuronal activity. fMRI allows the simultaneous detection of the entire neuronal population responding to each stimulus. However, since it provides an indirect measure of neuronal activity, obtaining a realistic estimate of the number of activated neurons requires a number of intervening steps.

Our approach was to use the extensive knowledge of the functional architecture of primate V1 as a "jumping board" from which a conservative estimate of the ratio between hemodynamic response and neuronal firing can be obtained. This ratio was then used, in addition to several cautious
assumptions, to assess the number of neurons, which respond to a single object image, in the entire visual cortex and particularly in object related areas (Fig. 1).

Figure 1: Diagram of the analysis steps
Steps 1 and 2 are used to calibrate the spikes/BOLD ratio. Steps 3 and 4 use this calibration on data from the region of interest (e.g. pFs) to assess a lower bound for the number of responsive neurons in this region.

Three stimuli were used in an event-related designed experiment. A moving rectangular-wave grating was used to maximally activate V1 neurons sensitive to a particular orientation (Tootell et al., 1998). Images of a single face and a single house were used to activate object-related areas. Despite the use of a single image, the resultant activation was quite large and widespread in occipital and temporal cortex (Fig. 2a). The grating elicited substantial activation in V1, as well as in higher-order areas (Fig. 2a left). The face image typically  preferentially activated a region in the posterior fusiform gyrus (pFs) corresponding to the FFA (Kanwisher et al., 1997) whereas the house image activated a region in the Collateral Sulcus (CoS), sometimes extending into the parahippocampal gyrus, corresponding to the PPA (Epstein and Kanwisher, 1998) (Fig. 2a right).
Both images also activated additional areas in occipito-temporal cortex as well as lower-tier areas (Hasson et al., 2003).

Figure 2: Single image activation maps and time-courses
(a) Activation to the moving grating (left) and the face (red) and house (blue) images (right) compared to blank. The right inflated hemisphere is presented from a lateral view for orientation purposes. Dotted lines mark borders of retinotopic areas. Color scales denote statistical significance. CoS, collateral sulcus; OTS, occipito-temporal sulcus; PCS, post central sulcus; pFs, posterior fusiform gyrus; STS, superior temporal Sulcus; Ant, anterior; Post, posterior. Note remarkably wide distribution of activation to single face and single house images. (b) Percent signal change elicited by the grating in V1 and V2. (c-d) Activation to the face and house images in the entire visual cortex (c) and in the pFs and CoS (d) in the right hemisphere sampled using an external localizer. Stimuli were presented at TR 0.
Below we describe the analysis steps and the assumptions used in the estimation of activated neurons (see Fig. 1).

**Step 1 – V1 neuronal activity.** Several parameters were used for this estimation. 1) The neuronal density of V1 was estimated, based on a recent study done in a large population of post-mortem human brains (Pakkenberg and Gundersen, 1997), as about 60,000 neurons/mm$^3$. 2) The fraction of neurons which may respond to a moving oriented rectangular grating was estimated based on electrophysiological studies (Hubel and Wiesel, 1968; O'Keefe et al., 1998). Considering that additional population of neurons may have been tuned to other stimulus attributes (e.g. color (Hubel and Wiesel, 1968)) and to spatial frequencies not contained in our stimulus (O'Keefe et al., 1998), we conservatively estimated the fraction of responsive neurons to the grating as between 20%-50%. 3) The response to a grating of a single orientation, out of the maximal possible response generated by all possible orientations, was assessed based on the orientation tuning curve of V1 neurons. The average tuning curve Half Width at Half Maximum (HWHM) was estimated as between 27º, based on monkey single units (O'Keefe et al., 1998; Ringach et al., 2002), and ~45º, based on deoxyglucose uptake (Malach, 1994), optical imaging in anaesthetized macaque (Bartfeld and Grinvald, 1992), and human fMRI (Tootell et al., 1998). Assuming a Gaussian tuning curve and a homogeneous distribution of orientation preferences, this means that on average, the population "spike contribution" of a single orientation grating is between 32% and 60% of the overall possible response (see Methods). The lower end of this range is also compatible with patchy lateral connections, which are likely to be correlated to iso-orientation domains, and also occupy about 30% of cortical territory (Malach et al., 1993). Combined with the estimate of orientation-responsive neurons this gives an overall percentage of between 6% and 30% of the
maximal response of the entire population. 4) V1 peak firing rate was estimated, based on electrophysiological data, as about 45 spikes/sec (Geisler and Albrecht, 1997).

Multiplying V1 neuronal density, the percentage of responsive neurons, the fraction of spikes out of the possible maximum and the peak firing rate, we can derive the number of spikes elicited in the highest activated voxels in V1 as between 172,800 spikes/sec/mm³ and 810,000 spikes/sec/mm³.

Step 2 – V1 BOLD signal. Voxels in V1, which were most significantly activated by the grating compared to a blank screen, were sampled (Fig. 2b). The average percent signal change across the full hemodynamic response (4 time points) was 0.6% ± 0.1% SEM, peaking at 1.0% ± 0.2%. For comparison, the response in V2 reached a somewhat lower peak (0.7% ± 0.2%).

Combining steps 1 and 2 (Fig. 1 top) we can conclude that 1% BOLD signal change in V1 roughly reflected between 300,000 and 1,300,000 spikes/sec/mm³.

Step 3 – BOLD response to a single object image. An external localizer was used to localize the entire extent of visual cortex, as well as face and house related regions, and the response of each ROI to the single face and house images was measured (see Methods). In the right visual cortex a volume of 21,000 ± 5,000 mm³, located in occipital and temporal regions, showed an average signal change of 0.10% ± 0.04% and 0.14% ± 0.03% for a single face and house respectively (Fig. 2c). In the pFs face-related region a volume of 700 ± 200 mm³ was activated at 0.14% ± 0.02% for the face and 0.02% ± 0.03% for the house (Fig. 2d left). Finally, in the CoS building-related region a volume of 500 ± 300 mm³ exhibited a signal change of 0.26% ± 0.05% for the house and 0.10%
± 0.07% for the face (Fig. 2d right). Left hemisphere activation was sampled in a similar fashion (not shown).

**Step 4 – occipito-temporal firing rate.** The typical maximal firing rate in high order object areas was estimated based on two sources. First, typical monkey IT responses is about 20 spikes/sec (C.R. Olson, personal communication). Second, single unit recordings in human middle temporal structures during natural viewing was estimated as 25 spikes/sec (R. Mukamel and I. Fried, personal observation). However, since representation principles in high order visual areas are still unclear, it could be that higher firing rates, up to those seen in V1 (45 spikes/sec), would have been obtained had the optimal stimuli been used.

Combining steps 3 and 4 with the ratio between neural activity and BOLD signal change (Fig. 1 bottom) we can now derive an approximation of the number of neurons which responded to single face and house images in the visual cortex in general (Fig. 3a) and in the pFs and CoS in particular (Fig. 3b). The calculation was done separately in each subject and in each hemisphere. Results for right and left hemispheres were averaged separately across subjects and then summed. Each estimate was calculated twice using either the most conservative or the most liberal values for each estimate (Arrows in Fig. 3, see Table 1 for a summary of the estimates).

The results show that a single face image activated between 30 and 300 million neurons in the entire visual cortex, of which between 1.1 and 12 millions were in the pFs face-related region (Fig. 3, dark purple bars). A single house image activated between 40 and 400 million neurons, of which between 2.2 and 23 millions were in the CoS (Fig. 3, dark blue bars).
Figure 3: Estimates of the number of neurons responding to a single image
(a) Entire visual cortex. (b) pFs and CoS. Estimates are based on percent signal change calculated in 3 ways (see Methods). Arrows denote lower and higher estimates using either the most conservative or the most liberal parameter values. Note that a single face image activates more than a million neurons in human face-selective cortex.

To ensure that the results did not depend on the specific manner in which the percent signal change was calculated we repeated the calculation using the averaged percent signal change of the two middle time points in each event (Fig. 3, middle bars) or the response peak (Fig. 3, rightmost bars). Very similar results were obtained. Thus we can conclude that at the minimum, a million neurons are activated in object-selective manner even when a single object image is perceived.

How reliable is the number we obtained? The estimation hinges on several intervening quantities, each suffering from a wide margin of error. Although such errors are negligible when compared to the huge number of neurons which turn out in the calculations, we always preferred to err on the conservative side. Thus, a similar hemodynamic response in V1 and in other visual areas was
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assumed, although blood vessels are denser in V1 (Zheng et al., 1991), which means that a similar neuronal activation can give rise to a higher hemodynamic response in V1 than in occipito-temporal cortex. This is suggested also by the lower activation level found in V2 (0.7% compared to 0.9% in V1) for the grating stimulus. In addition, we assumed stable responses over scan time in high order object areas, ignoring fMRI adaptation (Grill-Spector and Malach, 2001) which has probably lowered the signal produced by the face and house images along the course of the experiment.

The spikes to BOLD ratio in V1 calculated here is higher than reported previously (Heeger et al., 2000). However, since this ratio is based on the typical BOLD levels obtained in each lab, the crucial point is that activation in both V1 and occipito-temporal cortex was estimated in the same scan. Finally, the results are compatible with a recent study showing that the brain’s normal energy consumption allows a ceiling of about $3 \cdot 10^7$ concomitantly active neurons (Lennie, 2003). In the future, as more accurate approximations are obtained for each of the above steps, a more and more refined estimate of the number of neurons will be possible.

Our results bear important implications for “realistic” models of object representation. We found that out of about 50 million neurons in the pFs, at least a million (2%) respond to a single face image. Assuming an independent response of each neuron, this in principle enables the storage of more than $10^{2,000,000}$ different images (the number of ways to pick 1 out of 50 millions). Note that this is a conservative approximation, since it assumes an all or none neuronal response and a fixed size of the activated subset. Thus, from a combinatorial point of view this representation maximizes the memory capacity of the network leading to a truly stupendous number of possible representations. In contrast, sparse coding, using a representation of very few neurons, or a completely distributed one, using most of the neuronal population, would result in a largely reduced storage capacity.
Finally, it could be argued that within the highly distributed neuronal population, only the few neurons which are at the very peak of activation truly participate in each representation. At this point, we can not rule out this possibility. It should be noted though that the population of highly active neurons might be even more wide-spread than that defined by conventional fMRI, since recent adaptation studies suggest that even weakly activated voxels may contain highly active populations of neurons (Avidan et al., 2002).

Table 1: Values of previous data used for the estimates.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>V1 neural density [neurons/mm³]</td>
<td>60,000</td>
</tr>
<tr>
<td>V1 fraction of responsive neurons</td>
<td>0.2 - 0.5</td>
</tr>
<tr>
<td>V1 spikes out of maximum</td>
<td>0.32 – 0.60</td>
</tr>
<tr>
<td>V1 peak firing rate [spikes/sec]</td>
<td>45</td>
</tr>
<tr>
<td>Occipito-temporal peak firing rate [spikes/sec]</td>
<td>20 - 45</td>
</tr>
</tbody>
</table>

Each estimate was calculated twice, using either the more conservative values (leading to a lower number of activated neurons) or the more liberal values.

**METHODS**

**MRI Setup**

Subjects were scanned on a 1.5T Signa Horizon LX 8.25 GE scanner. In the main experiment a quadrature surface coil was used (Nova Medical Inc., Wakefield, Massachusetts), which covered the posterior brain regions. Blood oxygenation level dependent (BOLD) contrast was obtained with gradient-echo echo-planar imaging (EPI) sequence (TR = 1500ms, TE = 55ms, flip angle = 70°, field of view 24 × 24 cm², matrix size 80 × 80). The scanned volume included 13 nearly-axial slices.
of 4 mm thickness and 1 mm gap. In the localizer experiment a standard birdcage headcoil was used and the scanned volume included 25-26 slices to cover the entire cortical surface. Imaging parameters were as mentioned above, except for a TR of 3000ms and a flip angle of 90º. A whole brain spoiled gradient (SPGR) sequence was acquired on each subject to allow accurate cortical segmentation, reconstruction and volume-based statistical analysis. T1-weighted high resolution (1.1x1.1 mm) anatomical images of the same orientation as the EPI slices were also acquired to facilitate incorporating the functional data into the 3D space.

Subjects

7 subjects participated in the experiment (5 women, ages 22-46). Data of one subject were discarded due to excessive head motion and data of another subject were discarded due to problems in data acquisition. All subjects had normal or corrected-to-normal vision and provided written informed consent. The Tel-Aviv Sourasky Medical Center approved the experimental protocol.

Stimuli and experimental design

Stimuli were generated on a PC, projected via an LCD projector (Epson MP 7200) onto a tangent screen positioned over the subject’s forehead, and viewed through a tilted mirror.

Main Experiment

The experimental design was event-related. Three images were presented throughout the experiment, each repeating 30 times. The images were a face photograph, a house photograph, each subtending 10 deg of visual field, and a moving vertical grating in an annulus whose inner
diameter was 2.5 deg and outer diameter was 18 deg. The grating was rectangular – thin white stripes on black background. Spatial frequency: 1.1 cycle/deg. Duty cycle: 0.3. The grating moved randomly to left and right 16 times per sec. Movement range was between 0.25 deg and 0.7 deg. Each image was presented for 1 sec, followed by a 5 sec blank. Trials were counterbalanced. The experiment started with a 21 sec blank period, followed by 6 sec of pattern images, and ended with a 15 sec blank period, resulting in a total duration of 588 sec. Subjects were instructed to fixate on a red dot positioned at the center of the screen throughout the experiment and to covertly name the images.

**Localizer Experiment**

This experiment was used to localize object-related regions. Subjects were presented with 15 sec movie clip epochs containing either faces, buildings, navigation episodes or various objects. Such stimuli were previously found to be highly effective and to preserve the known selectivity of object areas (UH, Y. Nir, IL and RM *Hum Brain Mapp* (NYC, USA, 2003)). Each condition was repeated eight times. Epochs were pseudo-randomly ordered and interleaved with 6 sec blanks.

**Mapping borders of visual areas**

The representations of vertical and horizontal visual field meridians were mapped in all subjects in order to delineate borders of retinotopic areas (Engel et al., 1994; Sereno et al., 1995; DeYoe et al., 1996). Stimuli were presented in 18 sec blocks, interleaved with 6 sec blank periods. Images were presented for 250 ms in a consecutive manner. Stimuli consisted of triangular wedges that were presented either vertically (upper or lower vertical meridians) or horizontally (left or right horizontal meridians). Each condition was repeated four times. Two versions of the experiment were run. In the first, the wedges consisted of either gray-level natural images or black and white objects-from-texture pictures (Grill-Spector et al., 1998). In the second, the wedges consisted of
colored copies of objects superimposed on colored textures. Subjects were instructed to fixate on a small central cross.

**Data analysis**

fMRI data were analyzed with the BrainVoyager software package (R. Goebel, Brain Innovation, Maastricht, Netherlands) and with complementary in-house software. The first three images of each functional scan were discarded. The functional images were superimposed on 2D anatomical images and incorporated into the 3D data sets through trilinear interpolation. The complete data set was transformed into Talairach space (Talairach and Tournoux, 1988). Preprocessing of functional scans included 3D motion correction and high frequency temporal filtering. The cortical surface was reconstructed from the 3D-SPGR scan. The procedure included segmentation of the white matter using a grow-region function, the smooth covering of a sphere around the segmented region, and the expansion of the reconstructed white matter into the gray matter. The surface was then unfolded, cut along the calcarine sulcus and flattened. Statistical analysis was conducted on the flattened cortex.

**Statistical Analysis**

Statistical analysis was based on the General Linear Model (Friston et al., 1995). In the main experiment a gamma function predictor with a delay of 2.5 sec and a time constant of 1.25 sec was constructed for each experimental condition except blank, and the model was independently fitted to the signal of each voxel. A coefficient was calculated for each predictor using a least-squares algorithm.

A similar model was constructed for the localizer experiment, except that the function used to model each predictor was a boxcar function with a lag of 3-6 sec.
V1 most active voxels were defined as those in which the coefficient of the grating predictor was highly significant compared to zero. The threshold was individually selected for each subject such that the activated volume in V1 in each hemisphere did not exceed 1000mm$^3$. A similar criterion was used to define active voxels in V2.

Face and house related activation was first assessed searching for voxels in which the corresponding predictor coefficients were significantly different from zero (p<0.05).

The external localizer was used to define regions of interest (ROI's) for sampling activity to the face and house images. First, the entire extent of visually active areas was localized by contrasting the average of the four coefficients (faces, buildings, navigation, objects) with zero. Next, face and building related regions were localized by contrasting the face and building coefficients. ROI's were defined on the cortical surface as clusters of at least 50 mm$^2$ in which the p value of the test was less than 0.05. The pFs region was defined as activated voxels in the vicinity of the fusiform gyrus, anterior to retinotopic areas and the CoS ROI was similarly defined in the CoS.

**Time course analysis**

Time-course in each ROI was sampled and percent signal change compared to the blank period preceding it was computed in three different ways: averaging across the entire hemodynamic response (4 samples), averaging the two middle points of the hemodynamic response and using the response peak. Repetitions of each condition and all the time points in each condition were then averaged. Finally, results were averaged across subjects.

**Statistical significance**

Calculation of significance values in the activation map (Fig. 2a) was based on the individual voxel significance and on the minimum cluster size of 50mm$^2$ voxels (Forman et al., 1995). The probability of a false positive was determined from the frequency count of cluster sizes within the
entire cortical surface, using a Monte Carlo simulation (AlphaSim by B. Douglas Ward, a software module in Cox, 1996).

**Calculation of response fraction out of possible maximum**

The Half Width at Half Maximum (HWHM) of the orientation tuning curve reported in each study was used to estimate the total response to a grating of a single orientation, by integrating the area under the tuning curve. In the deoxyglucose study the tuning curve was derived from a line scan of autoradiographic photograph and in the fMRI study from indirect measure based on recovery from adaptation.

Assuming a Gaussian function this area is given by:

\[ A \int_{-\pi}^{\pi} e^{-\ln{2} \frac{x^2}{x_0^2}} \, dx \]

where \( x_0 \) is the HWHM and \( A \) is the peak firing rate.

The theoretical maximal possible response is obtained when all responsive neurons fire at their peak firing rate:

\[ A \cdot 2\pi \]

Dividing these two values provides an estimate for the response fraction out of the possible maximum.
References


Chapter 3
General Discussion

3.1 Topographic organization of object-related areas

The main finding of this thesis is a new organizational principle of object-related areas. We have found that almost the entire extent of object-related cortex is organized in a center-periphery organization, and that there is an association between specific object categories and certain visual field eccentricities. Thus, face-related regions (pFs and LO) largely overlap central visual field representations, whereas the building-related region (CoS) overlaps peripheral representations.

The finding of a center-periphery organization in object-related areas extends a previous report of a center-bias in LOC (Grill-Spector et al., 1998b). The exposure of an eccentricity map beyond the classical retinotopic areas is probably due to the use of object images as stimuli. Earlier studies have mapped the organization of early visual areas using a variety of texture patterns (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997; Tootell et al., 1997). Such patterns were presented either as rotating wedges, to map the polar angle, or as contracting and expanding rings, to map the eccentricity. While these stimuli are very effective in activating early visual areas, they are much less so for object-related cortex. Using object stimuli ensured that some level of activation will be obtained. Presenting the objects either in the center or in the peripheral visual field enabled us to reveal the modulation of object-related activity caused by eccentricity.

The eccentricity map in ventral occipitotemporal cortex unifies the center-biased pFs face-related region and the periphery-biased CoS building-related region into one entity, which we have termed Ventral Occipito Temporal (VOT) cortex (Malach et al., 2002). Later work of our group (Hasson et
al., 2003a) found that a dorsal building-related region located in the vicinity of the Transverse Occipital Sulcus also exhibited a peripheral bias. Together with the center-biased LO face-related region a dorsal complete center-periphery map was obtained, mirroring the ventral one. This second map was termed Dorsal Occipito-Temporal cortex (DOT). Given the close proximity of occipitotemporal object-related cortex to early visual areas, the center-periphery organization in both low and high order areas seems like a single continuous map.

### 3.2 Properties of the center-periphery organization

The iso-eccentricity bands in object-related cortex are a rough direct extension of the eccentricity map in lower visual areas. However, the high order eccentricity map was not as sharp as that found in early retinotopic cortex, where each cortical segment is activated exclusively by a specific part of the visual field. Rather, it appeared as an organization of eccentricity biases, in which each cortical region is preferentially activated by either the center or the periphery, but is also responsive to some degree to the rest of the visual field. This is especially evident when considering the level of activation to peripheral stimuli observed in central regions (e.g. Fig. 4b in (Levy et al., 2001)). Note, however, that the stimuli were constructed such that they compensated for the reduction in cortical magnification factor in the periphery of classically retinotopic areas. There is some evidence pointing to substantial changes in the magnification factor in high order areas compared to lower ones. In particular, the mid-periphery representation appears to be substantially shrunk (Levy et al., 2001; Tootell and Hadjikhani, 2001). Therefore it is notable that a very small stimulated area in the center yielded preferential activation in the pFs and LO face related regions compared to much larger peripheral stimuli.
Another major difference between high order and early visual areas is that in high order ones eccentricity is not an exclusive overall organizational principle. It appears that two types of organizing dimensions coexist in occipito-temporal object-related cortex: the eccentricity map and the organization of object categories. There is a consistent relationship between these two dimensions, but each can be revealed by keeping the other dimension constant. For example, presenting two groups of images that share the same shape category but differ in their location in the visual field (e.g. faces presented in the center of the visual field vs. faces presented in the periphery) will highlight their eccentricity organization. Conversely, comparing activation to images which differ in their features, but are presented in the same eccentricity distance (e.g. faces in the center vs. buildings in the center) will reveal the category-related organizations.

Despite these obvious differences between the eccentricity organization in low and high order areas, in some respects they are quite similar. First, in object-related areas, similar to lower areas, the eccentricity map was not specific to stimuli which preferentially activate each region, such as buildings in the CoS, but could be obtained even using the non-preferred stimulus. A likely source for this result appears to be the marked reduction in category-selectivity for peripheral stimuli observed in the CoS. Thus, the CoS showed a higher selectivity to building images when these images were presented centrally compared to when they were presented peripherally, although in terms of overall activation, the peripheral stimuli produced a higher activation level.

Second, the peripheral bias observed in the CoS was indeed related to the peripheral location of the stimuli, rather than to other properties of the peripheral stimuli, i.e. multiplicity of objects and large stimulation area. In the original experiments the central stimuli consisted of small objects presented in the center of the visual field, whereas the peripheral stimuli were comprised of several
enlarged copies of the same objects presented in a peripheral annulus, thus confounding peripheral location with large stimulation area and multiplicity of objects. The experiments described in chapter 2.2 explored the influence of these factors. One experiment produced the periphery effect using an enlarged single object filling the periphery. The effect was obtained even though the central and peripheral stimuli were identical in terms of shape and only differed in their size. A second experiment employed stimuli of equal area presented in mid or far periphery. The CoS was still preferentially activated by the more peripheral stimuli. Hence, the peripheral effect seems to be at least partly due to a true bias towards the peripheral visual field, similar to the case of lower areas.

Finally, it seems that the representation of objects along the eccentricity map is continuous rather than modular. A characteristic of the orderly topographic eccentricity map found in early retinotopic cortex, is that it changes smoothly along the eccentricity dimension. However, the high order eccentricity map found in occipitotemporal cortex was compatible not only with such a continuous map, but also with the possibility of a modular organization, which is "super-imposed" on an eccentricity- biased map. The results reported in chapter 2.3 are supportive of the former option, at least in the center-biased pFs. Front and back of the head images were mapped to largely overlapping, but consistently offset regions, in accordance with the notion that the fusiform gyrus contains a continuous, smoothly changing topography, rather than anatomically segregated, sharply defined modules. A modular organization should have been associated with more "binary" maps in which different object images are mapped either in complete overlap (in those cases where they belong to the same "module", or in a segregated manner (in those cases where they belong to different "modules"). The direction of the very slight offset (~1 voxel) revealed in the activation to front vs. back images was consistent across subjects, and thus cannot be attributed to
random variability. Rather, it suggests that there are no sharp modular boundaries and each object can occupy a different territory within a smoothly graded topography, depending on factors such as resolution demands.

### 3.3 Functional implications of the topographic organization

The new topography indicates that object recognition is not a uniform task, but one that engages functionally different processes. In particular, some processes require analysis of fine detail. Such processes include identifying individual exemplars within a category, identifying facial expression and gaze direction, etc. These aspects of object recognition naturally rely on high resolution input. In contrast, other processes, such as navigation, spatial orientation and texture segregation may depend more crucially on large scale integration or synthesis. Since foveal vision is closely associated with high resolution, whereas the resolution of peripheral vision is lower, it makes sense that processes of the first type will be linked to foveal vision and processes of the second type to peripheral vision.

This notion is supported by several lines of evidence suggesting that qualitatively different processes take place in the center-biased pFs and the periphery-biased CoS and PPA. A number of studies have implicated the pFs in object recognition, showing that this region singles out for detailed analyses specific objects of interest embedded in the visual scene. This is compatible with the center-bias found in this region, which implies higher resolution compared to the CoS, and with the results of a recent study, reporting higher activation to high-spatial-frequency faces compared to low-spatial-frequency ones (Vuilleumier et al., 2003). This high resolution enables a fine analysis of the visual information, leading to extraction of objects or features matching some templates that
are represented in this region. It should be noted that fine detail analysis does not imply that the pFs is involved in local rather than global recognition processes. On the contrary, several studies have shown that the response of this region is not feature-based, but rather holistic and correlated to object perception. Using the Rubin face-vase illusion, Hasson et al (Hasson et al., 2001) showed that pFs activation was significantly higher when subjects perceived the illusion as two profiles compared to when a vase was perceived, although local features were almost identical. Similar results were obtained by (Andrews et al., 2002). Tong et al (Tong et al., 1998) induced binocular rivalry by presenting a face image to one eye and a house image to the other. They showed that FFA activation was higher when a face was perceived compared to times in which a house percept was elicited. All these studies indicate a correspondence between the ability to recognize an image as a face, regardless of its identity, and pFs activation.

Two recent studies in congenital prosopagnosic subjects revealed normal selective activation in their face area compared to houses and common objects (Hasson et al., 2003b; Avidan et al., 2004). Since prosopagnosic patients are impaired at face identification but not at face detection these results may suggest that the pFs is involved in the latter process rather than the former. This is compatible with studies showing only a slight reduction in activation to inverted faces in spite of a marked reduction in identification levels (Haxby et al., 1999) as long as the image can still be recognized as a face (Kanwisher et al., 1998) (but see (Grill-Spector, 2003b)). However, in light of the center-bias found in face-related regions, the apparent lack of correlation between identification of individual faces and pFs activation may have another interpretation. It could be that the pFs is not engaged in face identification, but in other, subtler, tasks related to faces, such as identification of emotional expression and direction of gaze. These processes rely on higher resolution than face
identification (Schyns and Oliva, 1999), and therefore will be naturally expected to be associated with center-biased regions.

In contrast to the pFs, the PPA seems to be primarily engaged with the overall layout of the visual environment. This notion is supported by the findings that the PPA is highly activated by outdoor scenes, even more than by buildings (Epstein et al., 1999) and that it is sensitive to the spatial arrangement of the visual stimuli. Thus, the PPA was more activated by scenes containing no objects compared to objects with no spatial context and by intact room images compared to images which were fractured and rearranged (Epstein and Kanwisher, 1998). Furthermore, a recent study showed that the representation in the PPA is viewpoint-specific (Epstein et al., 2003), i.e. sensitive to changes in the spatial relationship between the scene and the observer. The peripheral effect found in the CoS is compatible with a role in navigation and representation of the spatial structure of the visual environment (Aguirre et al., 1998), which involve large scale integration of information across the visual field. Indeed, several neuropsychological studies (Landis et al., 1986; McCarthy et al., 1996; Aguirre and D'Esposito, 1999) described patients with medial occipitotemporal lesions, who suffered from an inability to use the visual appearance of places and landmarks for orientation purposes. However, both neuropsychological and imaging results so far are also compatible with the CoS having a more general role in spatial integration, which is required for navigation but can also be used in other tasks. The finding that the periphery-effect could be obtained for faces supports this notion.

The difference between the pFs and the CoS does not imply the existence of segregated modules. It is compatible both with a modular organization (Spiridon and Kanwisher, 2002) and with a distributed one (Haxby et al., 2001; Avidan et al., 2002a). The pFs and the CoS could either be two
distinct entities performing different processes or two extremes of one continuum which starts with high resolution and fine analysis and ends with low resolution and global synthesis. The results reported in chapter 2.3 support the latter possibility.

3.4 Other object categories

The topographic organization of object-related areas along an axis of resolution needs yielded testable predictions regarding the representation of other object categories. Obvious examples of objects whose recognition entails high resolution analysis of fine details are letters and words, and therefore we expected their cortical representation to be tightly linked to central visual field representations. Other objects, like furniture, cars or tools, are less tightly connected to either fine analysis or global synthesis processes, and probably involve a mixture of both. Hence, we expected the representation of such objects to be either more distributed or to lie in an intermediate area along the eccentricity axis.

Several subsequent findings in our lab confirmed our predictions. First, it was shown that words and letter strings activated central representations (Hasson et al., 2002). The word-related activation was separate from the center-biased face-related activation, exhibiting an opposite hemispheric lateralization. Second, common man-made objects preferentially activated an interim region between the face and house related region ((Hasson et al., 2003a) see also (Grill-Spector, 2003a)). Finally, representation of such man-made objects was more distributed compared to faces and buildings, activating both central and peripheral regions (Hasson et al., 2002). Moreover, it was found that the organization of VOT is mirrored by a similar organization in dorsal occipito-temporal cortex (DOT), starting with a peripheral building-related region in the vicinity of the Transverse
Occipital Sulcus (TOS), continuing with a common object related region in the vicinity of the Lateral Occipital Sulcus (LOS) and ending with a center-biased face related region in the Inferior Occipital Sulcus (IOS). In between the center-periphery maps of VOT and DOT, around the Inferior Temporal Sulcus (ITS) lies a vast cortical region which exhibits center bias as well as a category preference for common objects.

### 3.5 Possible sources for the center-periphery organization

The eccentricity map in high order visual areas seems like a smooth continuation of the one in early visual areas, and its layout is highly consistent across subjects. Thus, it is likely that the eccentricity organization is innate, rather than acquired. But what could be the source for the anatomical link between representations of object categories and visual field eccentricities? Eye movement studies (Yarbus, 1967) have shown that in free scanning of an image subjects foveate certain object categories more than others (Fig. 1). In particular, they tend to fixate on faces, thus leaving the environment, including landscape features and room interiors, to occupy the peripheral retina.

This close behavioral connection between object categories and visual field eccentricities raises the possibility that spatial attention effects might explain the parallel anatomical link. It could be that an object which is associated with close scrutiny, like a face or a word, automatically focuses the "spotlight of attention" (Posner, 1980) on the central visual field, whereas an image of a place gives rise to a broader spotlight. This would mean that the categorization observed in object-related areas is not due to segregated representation of different categories, but rather to a secondary effect of the eccentricity organization.
However, this hypothesis is very unlikely according to a study done in our lab (Avidan et al., 2003). In this study subjects were presented with face and house images, on which superimposed were small or large arrow heads. Subjects were instructed to attend to the direction of the arrow head, and thus had to shrink or expand their spotlight of attention regardless of the presented object (face or house). Still, face and building related regions maintained their object selectivity, indicating that attentional demands alone could not account for the category-eccentricity association. Thus, it seems that the association is due to object or shape selectivity established over long term processes.
The day to day experience of behavioral association between categories and locations may induce an anatomical link between the two. Gauthier et al (Gauthier and Nelson, 2001) have shown that visual experience can modulate activity in face-related cortex. Thus car and bird experts, having a long-term visual experience of these categories, have activation to cars and birds respectively in their face area (Gauthier et al., 2000). Moreover, even a short-term training in recognizing novel objects may be enough for these objects to activate face areas (Gauthier et al., 1999). These results have led the authors to propose that the face area is actually an area of expertise (Tarr and Gauthier, 2000). Since all humans are experts in face recognition, this area exhibits consistent preferential activation to faces. However, other categories of expertise can also activate the area.

The possible role of visual experience in the formation of face-related areas is stressed in a recent study (Lerner et al., 2003) which used fMRI to study subjects with developmental amblyopia - reduced visual acuity and contrast sensitivity in one eye. These subjects exhibited a significant reduction in pFs activation to face images viewed through the amblyopic eye compared to images viewed through the sound eye, but no similar reduction in activation to house images, or in lower areas activation. Other researchers have stressed the role of early visual experience on the layout of high order face-related areas. LeGrand et al investigated subjects born with a dense central cataract in both eyes (Le Grand, 2001) or in one eye (Le Grand et al., 2003) that prevented patterned stimuli from reaching the retina. They found that left, but not right, eye deprivation from birth until 2-6 months of age results in permanent deficits in configural face processing. The authors suggested that a critical period exists during child development in which visual experience leads to formation of face-related cortex.
Finally, it could be that the association between objects and eccentricities was formed during evolution, rather than development, such that specialization for object categories has become hardwired. This explanation is less likely in the case of words, since reading is a recently developed skill (a few thousand years). The possibility still remains that selectivity for different categories is established in different manners.

3.6 The nature of representation within object-related areas

fMRI experiments investigating object-related areas typically employ a vast number of stimuli from each category. A large cortical volume, in the order of hundreds of cubic mm, is usually activated by each category, implying the activation of tens of millions of neurons. How many of these neurons are activated by each single image? Using single face and single house images we found that at least a million neurons responded to a single object in occipito-temporal cortex, and that at least 30 millions were activated in the entire visual cortex.

These results are compatible with typical single-unit experiments, e.g. (Logothetis et al., 1995; Tanaka, 1996; Baker et al., 2002). In these experiments a relatively few (typically less than a hundred) stimuli are presented to a relatively small number of neurons, usually up to several hundreds, and yet at least one of the recorded neurons responds to at least one of the stimuli. Similar results have been obtained recently in humans (Kreiman et al., 2000).

The results have implications for computer models of object representation. They imply both a distributed object representation and a huge storage capacity of object-related areas, above and beyond what is typically assumed by conventional computer models. For example, in the pFs face-
related region, a million neurons out of 50 millions responded to a single face, according to the most conservative calculation. If different sets of a million neurons each are used to represent each image, a simple combinatorial calculation shows that $10^{2,000,000}$ different representations are possible.

It could be argued that out of the numerous responding neurons only a few which are most highly activated are the ones creating the perception of that object. Still, the other responsive neurons are also located at the highest stage of the object recognition pathway, and therefore must contribute in some way to the representation.

### 3.7 Future directions

Several directions for future studies arise from the results reported in this thesis. Some questions regarding the center-periphery organization remained open. First, the association between categories and eccentricities is not completely clear at the neuronal level. It could be that the same neurons that are selectively activated by a certain category (e.g. faces) also exhibit a bias to a certain magnification factor. However, due to the low spatial resolution of the fMRI, it could also be that the BOLD signal integrates the responses of two different neuronal populations, one selective to category and the other to eccentricity. High resolution fMRI methods, as well as intracranial recording may distinguish between these possibilities in the future. Second, the center-periphery organization yields testable connectivity predictions. Center-biased object areas should receive substantial input from foveal regions of retinotopic cortical areas, whereas periphery-based areas are expected to receive more information from peripheral regions. The newly evolved Diffusion Tensor Imaging (DTI) method (Kim and Garwood, 2003), which enables tracking of the axonal
fibers, can be used to test these predictions. Third, the center-periphery principle is probably not the single principle governing the organization of object-related areas. For example, it could be that these areas also contain a crude representation of the visual field meridians. It will be interesting to see whether such a representation also has a consistent relationship with different object categories. Finally, there is some evidence that the most anterior tip of object-related areas is not retinotopically organized. It could be that this region contains a more abstract representation of objects.
References


miyov shel azori עיבוד זורה בקורטיקס הוויזואלי
של האדם ור שימוש ב fMRI

hiyar l'shem kepalt Torah

Doktor lephilosophia

maa

Yifat Levi

Hagsh laqin haonibersiene haubiha bierishim

yonar, 2004
עבורה והנשחת בשירהך של
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פרופ' سورיה סולומון
תקציר

מחקרים רבים הרואים כי קילופトン המוח הא.webkitים-нима.destroyה של האדות מועברת בתהליך זה, שאובייקטים. מחקרים אלה חשו בפשר השטח הקורטיקלי, אך דפוס התמחות עשיר ומרוכב, שבאגורים שונים雾を利用ים יזור עד כך קוטגוריית מוסמוט של אוביקטים disasters על ידי קוטגוריית אחורות. הדגמנאות העיוניות והן צורות מופעלות זהות בסתיו התמחות התמחות עד לשישה מטרות, męskו מרсход התמחות של בניин ושטחית פחות. בתמחות אלה משקופות תופעה Grip, מחבר שקט shouting והגי-אנתומיים בני צורות, העיוניות בפרודTRS פסוחים שונים שנות ינש עקיבי מ裆 בקבוטריונים, שניים מביתם, צורות, העיוניות בתנועה ל entidad, הנמצאת בברחת collateral (pFs) fusiform gyrus.

העק ancor הנמנים בסיסי העיוניות תליית הקוטגורייה עדין, ייחודי, והן צורות, ניתן למד למד

gורמים הקשורים אלבר העובוקים, לשלשלת הקשתות בין והתמחות המוחית. בנוסף, אחד ממקורות המלחין ניתנים לספר בת Hispanics האנטומיים העקיבים בין הקוטגוריית השונות. בתוכו, יש לזכור כי התנגשה לכל קוטגורייהaina מוצלבת--+ hisseית: כל אזור התמחות

בקטגוריית אspNetותת, מבית בימי המשוערות עם הקוטגוריית אחורות, בער ילא רמה עד אפי

יוצר מבחר שלSpain הסוביקטים.

בחלק ההראה של העובד ממען עיקרון מהות, אשר יחול למספרי את העקיבי העובדיה של

התמחותים תליית הקוטגורייה. בלוחים השמיishi الكرונות את המאפים של אזור

הפרצופים והethoven המבגרים האגרוג הקולו הזה. בבתה, בחלק הרבעה, בתום את היינו של

אובייקטים בודק בוחר אゾרי, האויבקים של הערכונים את מספר הנינו העובדיה המשטחיפה ביוון זה.
הşturק היעקוב יוכל להתחבל עם ברוור פראופים, שלושה גייםvla-אוסטימאלי, עובר צורם.

ואלה. מסקננות היי צאורי, הבתים מגנים עליה רגישות נטענת עם השדה הראויים והיקפים

החרוזות על הכיתוב של עט פונוגרפי היא "יזג" בראקטים לאור צורק המרחק

המרחקים והם קרניים מודולארית של קוגנרטים ה"מלבוש" על פני המרחקים המוארים. על מנת
לבחון בו שיתוף הקוגנרטים מופנים את היצוגים של תצלומים קדומים של ראשיי, מתוכ
הנה ששויה של התמונות מתועלת בצורה חדית הקשורים זה לזו המרא, אך מתייחס
דרישות שלבעות אחורית ממד שי. הת nuesה את פעילות ב fMRI בשתי
וופיפמ שניות של של יתק לוחות ש損害 מקרית. דפוס פעילות זה אינו מתישב עם ארגון
מודולארית, שב צפה לתחיפה מחאה ואינו תיפוף לתחיפה של האזורים הפעילים. דפוס פעילות
משקף תופונגרפי ריצף, שב יזגיגים של צגמים הקשוים זה לזו "מחוקיק" על פני ה
fusiform gyrus.

המקחור האחזרו קושרן את 작은 הזת fMRI ל-April הפעילות העובדות והbastה הערכות של גבול
תחתיי וממצאים המשותפים בין צורק של ביאייק בודד. תוצרי fMRI ותצלומים פיסיולוגיים
על V1 שימש לכל היותר בן הפעילות העובדות וראוי fMRI. יישוב זה, ברצף ממסך החות
झירות, הופעל על גואת הצווארlys-טימרלייםชะי ל العشرות או הפעולים העובדות
בנתבגנה לאובקטיות. מצעים שונים לАЗיו צורק, ביאייקlys ואובקטים הולכים 30ミニון
וניצולים בככל הקוטקוטי תראית מערבים ביצוג של תומגנד אובייקט בודד, הנווטה שמדמה לע
"יזג" מבוחר בים.
# תочך העניינים

## פרק 1
**مبוא קליל**

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## רשימה סופרחת