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The topography of high-order human object areas

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Cortical topography is one of the most fundamental organizing principles of cortical areas. One such topography – eccentricity mapping – is present even in high-order, ventral stream visual areas. Within these areas, different object categories have specific eccentricity biases. In particular, faces, letters and words appear to be associated with central visual-field bias, whereas buildings are associated with a peripheral one. We propose that resolution needs are an important factor in organizing object representations: objects whose recognition depends on analysis of fine detail will be associated with central-biased representations, whereas objects whose recognition entails large-scale integration will be more peripherally biased.

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Topographic mapping is a ubiquitous property of sensory and motor cortex: there is an orderly and gradual change in some functional property of cortical neurons laid along the cortical surface. However, the topographical map is never a simple copy of the sensory surface, rather it undergoes complex and precise transformations, along well-defined organizing principles. This striking phenomenon has prompted the suggestion that topographic transformations might serve to facilitate specific cortical computations (e.g. [1,2]).

This conjecture is compatible with a more general perspective in which cortical neuroanatomy and mapping principles are treated as computational devices [3].

From this perspective, the interest in visual cortex topography stems not only from its use as a principle that defines the layout of many visual areas, but rather in providing important insights concerning the actual computations and optimizations performed by cortical networks. In this sense, the information about 'where' things occur in the cortex is highly relevant to knowing 'how' cortical computations are performed.

The basics of visual cortical topography

The topographic transformation from the retina to the cortical surface has been amply documented both in non-human primates (e.g. [4]) and, more recently, in human early visual areas, using functional magnetic resonance imaging (fMRI) [5–7]. A consistent finding in all these studies is that the mapping principle involves a topographic

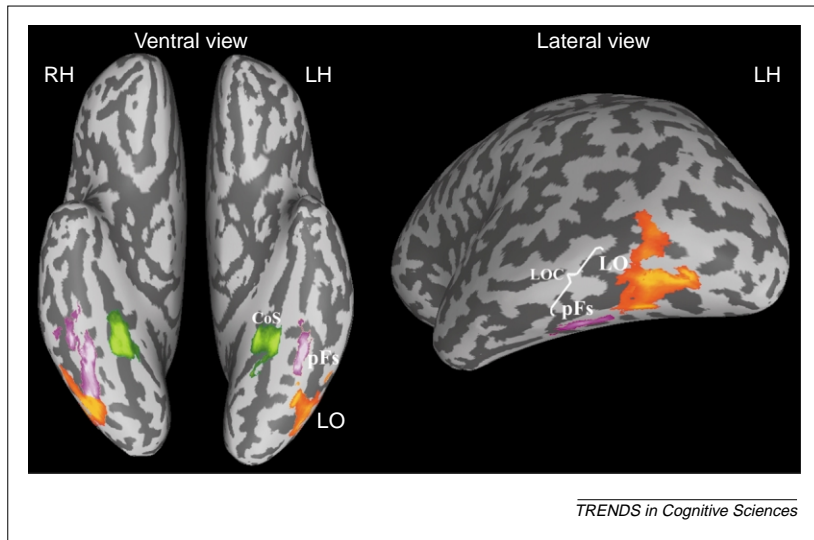


Fig. 1. Occipito-temporal object-related areas in the human ventral visual pathway. Location of high-order object areas is shown from a ventral view (left) and posterior-lateral view (right) of 'inflated' hemispheres. The regions include the dorsal-lateral-occipital (LO, orange) and the ventral-posterior-fusiform (pFs, purple) areas, which together form the lateral occipital complex. More medially, along the collateral sulcus (CoS) and parahippocampal gyrus, is located an additional region, which is reported to be sensitive to images of buildings and scenes (green). Results shown are an averaged map of 14 subjects.

transformation from a Euclidean coordinate system in the retina to polar coordinates in the visual cortex.

In this transformation, each of the early visual areas maps the visual field along two orthogonal axes: polar angle and eccentricity. Retinal points that lie on a specific radius whose origin is at the fovea have identical polar angle. Such radii are mapped onto parallel bands across cortical areas. The sequential layout of these bands reverses when crossing from one visual area to another, so that the relative position of the vertical and horizontal meridians alternates and provides an accurate delineation of the borders of these areas [5-7].

Along the orthogonal axis, retinal points that share the same eccentricity (i.e. lie on a ring centered at the fovea) are mapped onto a series of parallel bands that are orthogonal to the vertical and horizontal meridian representations. Crucially, a striking functional specialization is associated with the eccentricity axis: the amount of cortical tissue dedicated to the representation of a unit distance on the retina – the magnification factor – is inversely (and logarithmically) related to its eccentricity; so that foveal regions are characterized by an extremely large cortical magnification [5,7].

The dramatic increase in magnification factor in the fovea actually originates at the retina and reflects a profound foveal specialization for the analysis of fine, high resolution, detail. By contrast, peripheral parts of the retina are mapped coarsely on the cortical surface, so that large retinal (and visual field) distances are mapped on relatively nearby points in the cortical surface. It is interesting that although

this specialization is perhaps the most profound in the visual system, it has rarely been considered in models of object recognition.

The organization of human object representations
In the past few years, neuroimaging techniques of human visual cortex, in particular positron emission tomography and fMRI, have begun to dissect out not only the organization of early visual areas, but the more high-order and less topographically organized parts of visual cortex. These studies have revealed a rich and complex specialization pattern within occipito-temporal cortex. Particularly relevant for the present discussion are the early findings that consistently revealed a large cortical expanse, located at the lateral and ventral aspects of occipito-temporal cortex, which show functional specialization very suggestive of a role in human object representation and recognition. Thus, Malach *et al.* ([8], see also Ref. [9]) have described a large cortical region that they hypothesized might actually be a complex of several subdivisions, located at the lateral and ventral aspects of the occipital lobe, termed the lateral-occipital complex (the LOC). This large region was defined functionally by its preferential activation in response to a variety of complex object shapes (including faces and abstract 3D forms) compared with a large array of textures and noise patterns.

Anatomically (see Fig. 1), the LOC has been 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). The functional properties of the LOC include convergence of different visual cues [10,11], substantial positional and size invariance [12], completion and grouping processes [13-15], and, finally, correspondence to recognition performance [16,17]. These properties indicate that the LOC is a high-order cortical region that shows substantial specialization for object representations [18].

Recent studies have demonstrated that different cortical regions within the occipito-temporal cortex show preferential activation to particular object categories compared with others. Prominent examples include a region showing relatively enhanced activation in response to face images, termed also the fusiform face area (FFA) [19-22], as well as a cortical region sensitive to images of buildings and scenes (parahippocampal place area, PPA) [23,24]. Additional object categories such as tools [25], animals [25], the human body [26] and even chairs [27] have been reported to manifest specific and differential activation patterns.

The anatomical location of the face-related regions overlaps with the ventral subdivision of the LOC (the posterior fusiform gyrus), whereas the building-related region is situated medial to the LOC in the collateral sulcus (CoS), extending into the parahippocampal gyrus (see ventral view in Fig. 1).

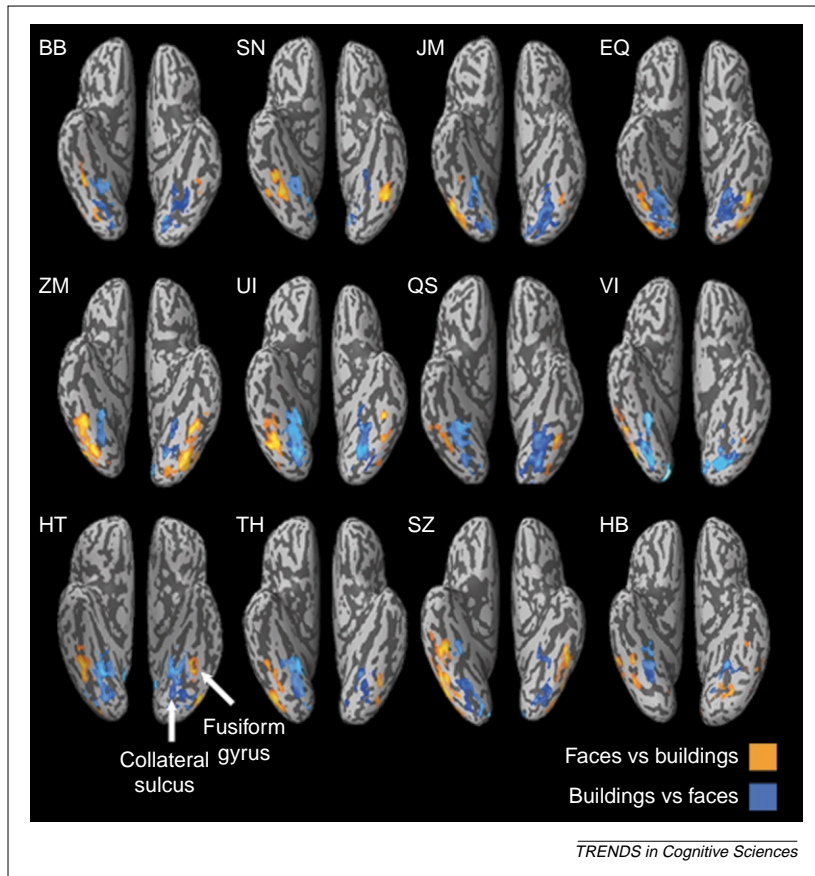


Fig. 2. Neuroanatomical consistency of differential category-related activation. Shown are 12 'inflated' brains in which the relative activation for face (orange) and building (blue) images was delineated. Note that despite substantial inter-subject variability, the preferential activation to faces was consistently located laterally, which suggests a general and robust organizational principle.

These category-related activations clearly reflect a robust phenomenon, as the neuroanatomical relationships between the functionally specialized regions are highly consistent across subjects and studies. For example, considering the differential pattern of activation to images of buildings and faces (Fig. 2), we can see that, despite substantial inter-subject variability, the preferential activation in response to faces is invariably located lateral to the activation in response to building images.

Although the category-specific specializations mentioned above are consistent, a difficulty arises in their interpretations. The main difficulty stems from the numerous potential parameters that can differentiate between different object categories. A non-exhaustive list includes shape factors, task-related factors and visual expertise effects (see Box 1). Thus, the cortical specialization revealed by neuroimaging studies can result from either one or more of these factors. It should also be noted that the response to specific categories is by no means absolute: each specialized region shows substantial activation in response to other object categories (although to a lesser extent), which might hint at a more distributed type of object representation [8,27,28].

Topography of occipito-temporal, object-related regions

All of the putative organization principles (Box 1) fail to account for the strikingly consistent neuroanatomical relationship between the different object-related activation patterns. Thus, an underlying organization rule that will put the different patterns of activation within the context of an overall principle is requisite.

Most previous attempts at deciphering the putative organizing principles of object representations focused on the functional properties of these regions. This article addresses this issue from a different angle by examining the neuroanatomy of high-order object areas. More specifically, we examine how the topography of their representation is related to the overall organization of the visual cortex.

Such a 'bird's eye' view is best obtained by examining the data on an unfolded representation of the cortical surface. To achieve this goal, the cortical surface is reconstructed and then inflated to expose its hidden curvatures. Then, a virtual 'cut' is made along the calcarine sulcus, which serves to unfold the inflated brain [5,29].

When examined in this fashion, it became obvious that high-order object areas are adjacent to early retinotopic areas, being close neighbors to areas V4–V8 (see Fig. 3). High-order object areas thus appear to form a natural extension of early retinotopic cortex – rather than an isolated entity. Given this close relationship, an appealing assumption would be that specific principles of topographic organization present in early visual cortex might extend anteriorly and 'spread' into high-order object areas.

Eccentricity map in high-order object representations

Early studies have mapped the organization of early visual areas using a variety of texture patterns [5,6,7,30]. Such patterns were presented either as rotating wedges, to map the polar angle, or as contracting and expanding rings, to map the eccentricity. Although these stimuli are very effective in activating early visual areas, they are much less so for object-related cortex. In an attempt to reveal topographic organization principles within higher order object regions, visual stimuli have been used in which the conventional texture patterns are replaced by object shapes known to enhance the activation in these areas [31].

Examining the LOC responses revealed that it manifested significant bilateral activation (from both visual hemi-fields [31]). Such a response profile argues against a simple retinotopy in the LOC, as conventional retinotopy entails mainly unilateral activation (from the contralateral hemi-field). However, in the same study, preferential activation in response to images presented centrally (foveally) was found, when compared with responses to more

Box 1. Putative organizational rules that could account for the category-related specializations in high-order object areas

There are at least four different dimensions that can account for the category-related activation found in the occipito-temporal object related regions.

Shape-related differences

Images from different object categories (e.g. faces and houses) are visually different. However, different exemplars from the same category tend to share similar visual features. Assuming that similar features are represented by neighboring neurons [a], then objects that have similar shapes could activate the same object-related cortical regions. Thus, selective activation for different sets of stimuli stems from the visual feature resemblance between different exemplars of each category.

Category-specific modules

This principle implies that there could be a specialized and independent module for the visual recognition of each object category. Such organization might be optimal because, presumably, different object categories necessitate different specializations in their representations. However, it is obvious that there is not enough cortex to support all putative object categories. Thus, a more restricted suggestion is that some categories, such as faces, letters and buildings, might be unique in having a specialized neuronal representation [b].

Task-related processing

Different object categories differ not only in their shape but also in their use. For example, objects might be used for spatial orientation (such as in navigation), for manipulating other objects (tool use), for social and parental interaction (face recognition), and for reading (letter recognition). Thus, it is possible that object representations are clustered not according to their physical visual characteristics, but according to their most common use. Such organization could facilitate optimal connectivity to higher level, action-related centers.

Expertise

A different dividing line between various object categories could relate to our ability to rapidly and efficiently recognize certain objects, and

particularly to the degree of visual 'expertise' in remembering and differentiating individuals within a category. A particularly striking example of such expertise is manifested in human face recognition. It has been argued [c] that the differential activation in ventral stream object areas is actually due to different levels of expertise in recognizing some objects (such as faces). This claim is supported by the findings that training subjects to become experts in recognizing particular object categories enhances activation in the fusiform face area to these categories.

Distributed representation

Finally, a completely different perspective is that objects are represented in a distributed fashion across the entire constellation of object related regions [d]. Neuroimaging data indeed demonstrate that the category-related specializations are often manifested as mild activation biases [e, f]. And there are theoretical advantages to such distributed schemes [g].

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peripherally presented images. Could this central bias be a part of a larger topography that is organized according to eccentricity?

To examine this issue directly, special eccentricity-mapping stimuli were constructed that were made out of rings of object shapes to enhance the activation in object areas. Examples of the stimuli used in the experiment are shown in Fig. 4a. Note that as in conventional retinotopic maps, the images were scaled with eccentricity to account for the drastic reduction in magnification factor with eccentricity. Interestingly, essentially the entire extent of high-order object areas, with possible exception of very anterior foci, appeared to contain an orderly map of eccentricity (see Fig. 4b).

When related to early retinotopic cortex, it clearly appeared that the eccentricity bands in high-order object representations were actually a rough extension of the global eccentricity map of early visual areas [32]. However, in contrast to early retinotopic cortex, the high-order eccentricity map was not as sharp and clean-cut. It appeared more as an organization of eccentricity biases, so even within the high-order central visual-field representation, one could find a consistent, albeit relatively reduced, activation by peripheral stimuli.

Within the high-order eccentricity map, it appeared that retinotopic selectivity was more pronounced in the posterior regions and became weaker at the most anterior regions. Thus, LO showed a higher degree of central-field bias compared with the pFs, and the posterior part of the collateral sulcus was more periphery biased than the anterior part.

The link between objects and eccentricity

The natural question that emerges from this analysis is 'is there a general principle that associates a specific eccentricity profile with each object category?' This question has been addressed by examining one of the best-studied examples of category-specific specialization: the differential activation in response to images of houses and faces. Recall that this activation pattern shows a consistent, and unexplained, medial-to-lateral segregation (Fig. 2). Within the context of the eccentricity map, it was examined whether there was a consistent relationship between the activations in response to faces and buildings, and specific eccentricity distances.

The answer to this question is presented in Fig. 5. Here, face-related regions [red borders in (c)] were defined as those activated preferentially by images of

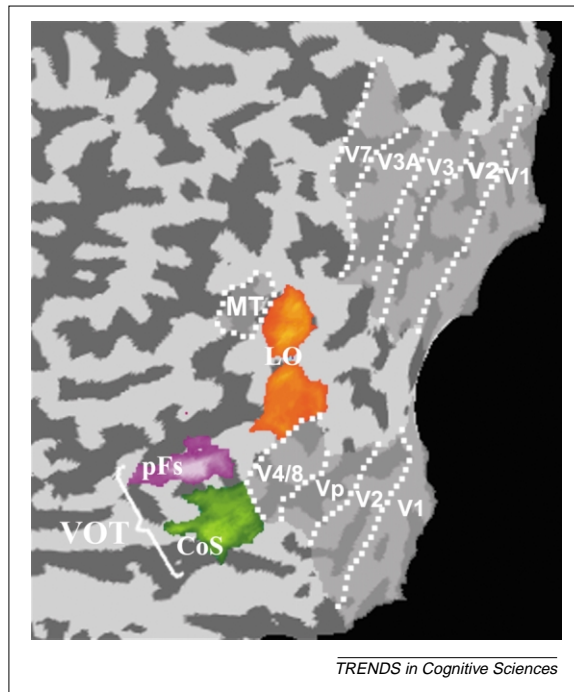


Fig. 3. A new scheme for the topography of human object areas. The layout of object-related cortex (colored regions as for Fig. 1) is indicated relative to early retinotopic areas (gray), which are defined by the location of their visual field meridians (broken lines). Note that the object-related regions closely adjoin early retinotopic cortex and appear to form a continuous entity. It is proposed that all the ventral occipito-temporal, object-related regions that stretch from the parahippocampal gyrus medially (green) to the fusiform gyrus and occipito-temporal sulcus laterally (including the pFs subdivision of LOC, purple), belong to a single entity termed ventral occipito-temporal cortex (VOT). LO (orange) is a separate entity located more dorsally and posteriorly to VOT.

faces compared with images of buildings, whereas building-related regions (blue borders) showed the opposite preference. Both faces and buildings were presented at the same location in the visual field. As can be seen, faces were consistently associated with central visual-field bias (yellow), whereas buildings were associated with peripheral visual-field bias (green). What could be the reason for such association between face- and house-related activation and eccentricity?

Eccentricity is tightly linked to acuity demands

At this point, we can only speculate about the significance of this new topography. It certainly highlights the fact that object recognition is not a uniform task: it engages different, often conflicting, processes. In particular, there are processes that require close inspection of fine detail; such processes include identifying subtle individual variations within a category, identifying gaze direction and emotional expression in faces, etc. It will be natural to process these aspects, at least initially, in cortical regions that receive a strong input from high-resolution, foveal representations. By contrast, there might be processes, such as navigation using terrain contours, texture segregation and spatial

orientation, that depend more crucially on large-scale integration. These functions might be better served by a strong association with peripheral, low-magnification representations.

Following this logic, it may be possible to derive testable predictions regarding the representation of other object categories. Clear segregated representations should be provided by objects that specifically require either high or low image resolution. Obvious examples of the first category are letters and words, because reading is a highly foveal task. Thus, the prediction is that the cortical representation of letters and words should be tightly linked to central, and not peripheral, visual-field representation. This prediction has been tested directly and observations indicate a clear association between letter-related activation and central visual-field bias [33].

Other object categories might tap both high- and low-resolution processing, and thus will be expected to occupy a more distributed representation, which could also include mid-eccentricity representations. Thus, images of common objects, such as tools and chairs, are likely to occupy a more intermediate or distributed association with eccentricity. This conclusion is compatible with the recent report that a large number of object categories, with the exception of body parts, do not show a localized activity pattern [26]. The localized representation of body parts makes it an interesting category in which to explore the relationship to eccentricity. One would expect it to occupy a mid-eccentricity position, and the fact that this representation is segregated from that of faces is compatible with this possibility, but of course does not prove it.

To summarize, it appears that two types of organizing dimensions co-exist in occipito-temporal object-related cortex: the eccentricity map (Fig. 4) and the organization of object categories (Fig. 5). 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 have similar shapes but differ in their location in the visual field (e.g. faces presented in the center of the visual field versus faces presented in the periphery) will highlight their eccentricity organization. Conversely, comparing activation to images that differ in their object category, but are presented in the same eccentricity distance (e.g. faces in the center versus buildings in the center) will reveal the category-related organizations [33,34].

It is important to emphasize that the eccentricity organization is not necessarily the exclusive organizational rule in high-order object areas, and many additional dimensions (see Box 1) might guide further subdivisions. For example, it is clear that letters and faces have reciprocal hemispheric lateralizations, with face representations emphasized more in the right hemisphere, whereas letters are emphasized more in the left hemisphere, although

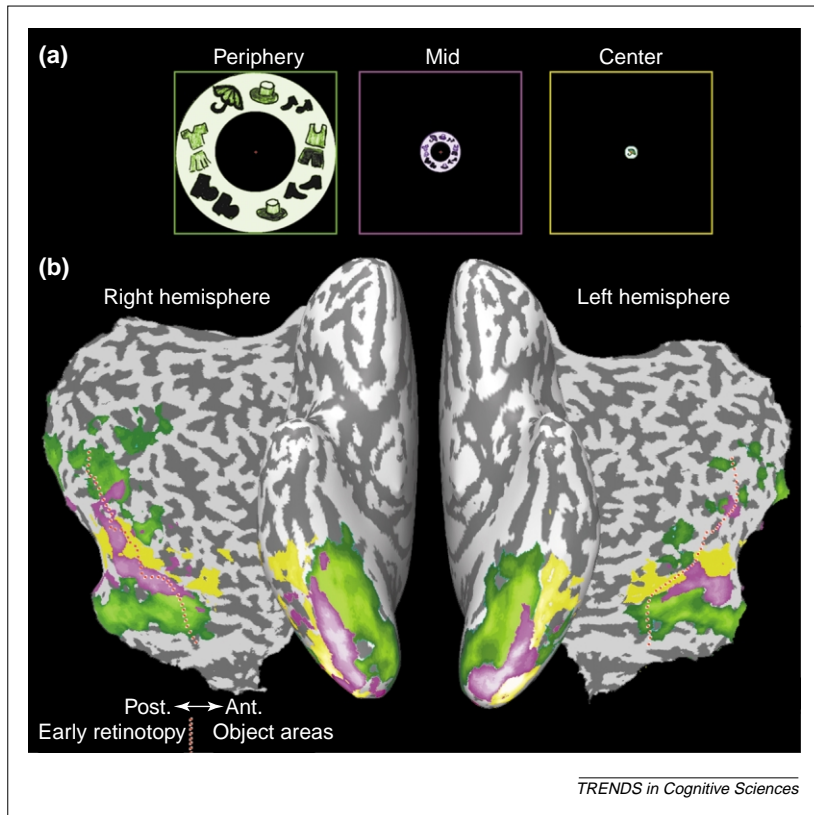


Fig. 4. Eccentricity organization of human visual areas. The orderly layouts of center (yellow), mid (purple) and peripheral (green) visual field representations (a) are shown on a ventral view of the inflated hemispheres and on an unfolded cortical format (b). Note that the eccentricity organization extends throughout the entire extent of human visual areas, including occipito-temporal cortex. The organization appears strikingly continuous across its entire extent, which suggests a global organizing principle. Results are an averaged map of 12 subjects.

both categories occupy central visual-field representations [33].

A new scheme for the organization of occipito-temporal object areas

The fact that face and building-related regions now appear to belong to a single eccentricity map has important implications regarding the organization of human occipito-temporal cortex. Thus, all anterior ventral object selective regions, which extend from the parahippocampal gyrus and collateral sulcus (anterior to V4–V8) medially, to the pFs subdivision of the LOC and further laterally into the occipito-temporal sulcus, can be considered as specialized subdivisions of a single entity. We propose that this entity be termed VOT (ventral occipito-temporal cortex) (see Fig. 3). More dorsally and posteriorly, region LO appears to constitute a separate entity, having both center and peripheral representations [32,35]. This region manifests a higher retinotopic sensitivity and more diffuse or complex object category modularity. Although the functional characteristics of LO and VOT suggest a sequential, hierarchical relationship between them [32], the possibility that these regions constitute parallel specialized representations cannot be ruled out at this stage

[36]. Finally, it should be noted that more anterior to VOT, an additional object-related cortex appears to lie, the eccentricity bias of which is variable and not fully resolved at present [17,32,37]

Resolution-based topography and holistic representations

Although not explicitly stated, the hypothesis that specific object categories segregate according to acuity demands has strong implications related to the nature of object representations. More specifically, for the linking between specific objects and eccentricity to be tangible, one has to assume that the neuronal representation can differentiate explicitly between object categories. Such a link cannot be established if the object representation is based solely on local, simple, object features. Thus, it is hard to conceive how a link between, for example, house images and a peripheral visual field could be established in a representation consisting of simple features that are common to houses and faces. Consequently, category-related differentiation can be accomplished only if the representation is sufficiently 'holistic' – that is, if the neurons in such a representation are sensitive to object templates or to object fragments that are sufficiently complex to be selective to particular object categories. Supporting this reasoning are several recent studies that indeed demonstrate that the representation in high-order object areas goes beyond strictly local image features, and codes for a more global shape representation [15,38,39].

Eccentricity and visual perception

Within the perspective of eccentricity specialization, specific well-known visual phenomena take on a new meaning. A striking psychophysical illustration of the sharp dividing line between central and peripheral visual recognition processes is provided by the phenomenon of 'crowding', in which peripheral integration of a group of items actually inhibits the identification of individual items. Interestingly, it has been demonstrated recently that, although the information about individual items is inhibited, it does influence the 'averaged' appearance of the items, which suggests large-scale integration associated with crowding in the periphery [40].

Another related phenomenon is the pattern of scanning eye movements that are performed when subjects are confronted with an image. Since the classic work of Yarbus [41], it has been clearly demonstrated that human subjects tend to foveate some object categories more than others. In particular, when the eye movements of a subject are carefully measured, they show a consistent, almost reflexive tendency to point their fovea at faces and to point their peripheral retina at landscape features and room interiors (see eye movement pattern in Fig. 6).

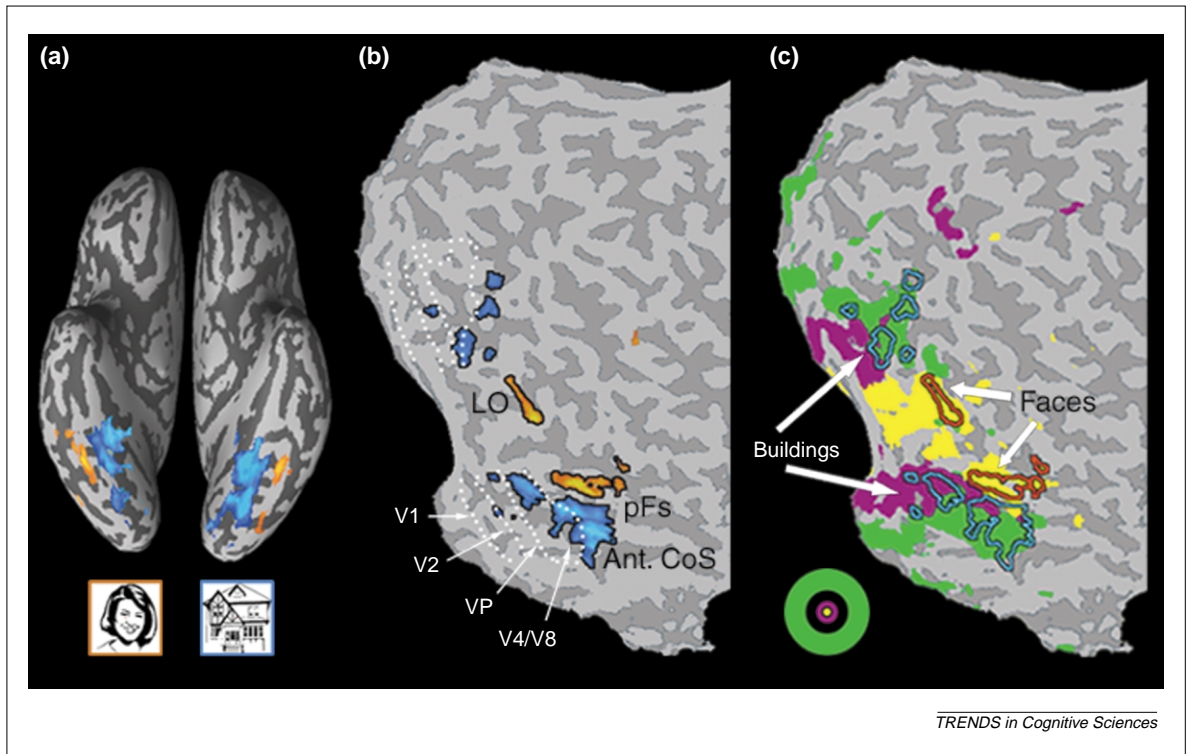


Fig. 5. Relationship between face- and building-related activation and visual field eccentricity. The preferential activation to faces (orange) and buildings (blue) is shown on a ventral view of inflated hemispheres (a) and on an unfolded cortical format of the right hemisphere, relative to borders of retinotopic visual areas (b). The borders of these regions are then superimposed on the eccentricity map (c). Note the close association between face-related activation and central visual-field bias (yellow), and the complementary association between building-related activation and peripheral visual field bias (green). Modified, with permission from Ref. [32].

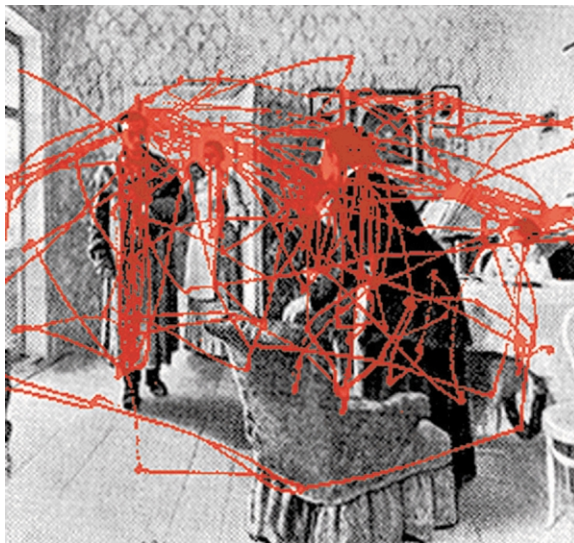


Fig. 6. Category preference of foveating eye movement. This classical image from the work of Yarbus depicts the location of the fovea of a subject while scanning a painting. Note the striking tendency to position the fovea on the faces within the picture. As a consequence, the contours of the room are preferentially positioned on the peripheral retina. It has been proposed that the eccentricity organization might provide a natural device for such linking between specific image categories, such as faces, and foveating eye movements. Modified, with permission, from Ref. [41].

The finding of center–periphery organization provides an elegant neuroanatomical mechanism that could explain this oculomotor behavior. By associating object categories with specific field eccentricities, a neuroanatomical network is naturally set for automatic guidance of foveal or peripheral vision to specific object categories. All that is required to complete such a network is a topographic mapping of connections from the eccentricity map to oculomotor centers – most likely via the parietal lobes [42] – and a direct link will be established between, say, face images and foveating eye movements. For example, when an image of a face is presented, it will activate the fusiform central visual-field representation. This central field representation, in turn will activate foveating eye movements through the hypothetical oculomotor link, which in turn will lead to the creation of a high-resolution, foveal, image of the presented face.

Even classical examples of visual illusions can be seen in a new light. Consider, for example, the rabbit–duck illusion (Fig. 7). Note that the perception of a duck’s face or a rabbit’s face is completely dependent on the location of the fovea relative to the specific part of the image: a face percept is ‘created’ only when the relevant image is brought to central field by fixating on a red cross. Conversely, this face percept is ‘erased’ if the same image part is now moved to the periphery by fixating the other cross.

Eccentricity organization and visual experience

Finally, these findings are relevant to a major issue that is of current central interest: to what extent the organization of object areas can be ascribed to innate

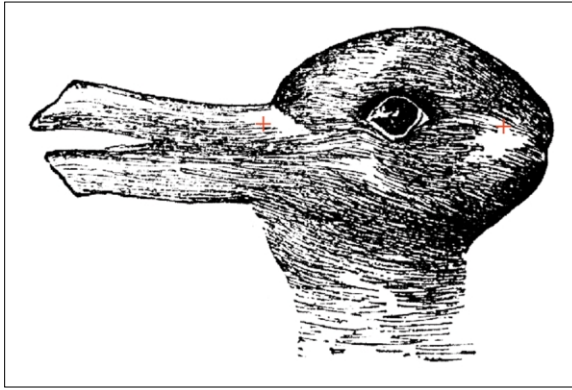


Fig. 7. The classic rabbit-duck illusion (originally noted by Wittgenstein). Note that the perception of this ambiguous image decisively depends on foveal location. Thus, the perception of a duck face is generated if the fovea is placed on the left cross, whereas the perception of a rabbit face is generated by placing the fovea on the right cross. Thus, there is a clear interplay between the visual-field location of images and their perceptual interpretation.

factors, and to what extent it is laid out and modified by postnatal visual experience? Examining the eccentricity map in high-order visual areas gives a strong impression that it is an organization that smoothly continues from early visual areas to high-order ones. Furthermore, the gross layout of this map is highly consistent across subjects. Thus, it is likely that the eccentricity organization is innate and is not modified by visual experience, although, as for many cortical organizations, it could depend on normal visual experience for its proper development [43]. However, it is certainly possible that the association between some object categories and a specific eccentricity might be strongly guided by visual experience and the 'visual expertise' of the subjects.

The studies of Gauthier and colleagues [44,45] are certainly compatible with this notion, as they show that activation in face-related cortex can be modified by experience. However, it remains to be seen whether activation in peripheral-biased cortex can also be modulated by experience.

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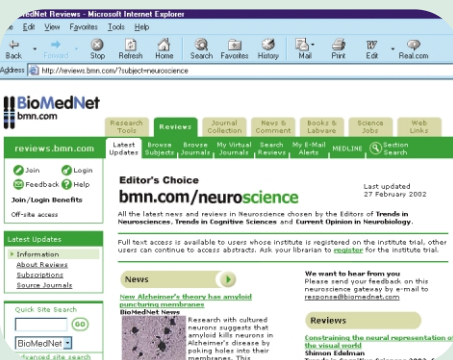
Questions for future research

- Are all eccentricities mapped uniformly in the high-order eccentricity representation – or are central and peripheral representations perhaps overly emphasized [35]?
- Can the association between object category and eccentricity be modified by visual experience?
- What precise recognition processes are associated with high and low acuity computations?
- How is information from disparate regions of the eccentricity map integrated to form a unified object representation?
- What are the additional topographical principles, unrelated to eccentricity bias, that guide the layout of object representations?
- What topographic principles guide the organization of dorsal shape-related regions?

Conclusions

This article proposes a new organizing principle of human high-order object areas that is based on an orderly layout of visual field eccentricity. The proposed scheme stems from the finding of a topography in high-order object areas, in which eccentricity bias, magnification factor and specific object shapes are linked in an orderly manner. Two such eccentricity maps are proposed: a posterior dorsal one, LO, located in lateral occipital cortex; and a ventral anterior one, VOT, in the ventral occipito-temporal cortex. Object categories, which appear to engage the analysis of fine detail such as faces and words are associated with central (high-magnification factor) representations. Objects whose recognition involves integration of visual information over large retinal distances, are mapped onto more peripheral, low-magnification factor representations. These findings can be summarized by a global principle in which acuity resources are mapped topographically in object areas. Different visual processes link to these resources according to their acuity demands, which leads to the observed, differential, activation maps.

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