The neural basis of object perception

Kalanit Grill-Spector

Humans can recognize an object within a fraction of a second, even if there are no clues about what kind of object it might be. Recent findings have identified functional properties of extrastriate regions in the ventral visual pathway that are involved in the representation and perception of objects and faces. The functional properties of these regions, and the correlation between the activation of these regions and visual recognition, indicate that the lateral and ventral occipito-temporal areas are important in perceiving and recognizing objects and faces.

Addresses
Department of Psychology, Jordan Hall building 420, Stanford University, Stanford, CA 94305, USA
e-mail: kalanit@psych.stanford.edu

Abbreviations
FFA   fusiform face area
PPA   parahippocampal place area
VOT   ventral occipito-temporal

Introduction

Humans can recognize an object within a fraction of a second. The neural mechanisms underlying this remarkable ability are not well understood. A promising strategy for attempting to understand human visual recognition is to characterize the neural system that accomplishes it — that is, the ventral visual pathway. This system extends from the occipital lobe into ventral and lateral regions of the temporal lobe.

Here, I describe recent findings from neuroimaging studies of humans that have examined cortical regions involved in visual perception of faces and objects. The findings from these studies have begun to elucidate the general organization and functional properties of these regions. I focus on two main issues in this review. First, what is the functional organization of the human ventral visual pathway? Second, what is the role of these regions in visual object recognition? I will show that ventral occipito-temporal (VOT) and lateral occipito-temporal object-selective regions are involved in representing

the shape of an object and are correlated with perceiving objects in many different recognition tasks.

Object-selective regions in the human brain

Object-selective regions respond strongly when subjects view pictures of objects but not when they view pictures of textures, noise or highly scrambled objects. These regions comprise a large constellation of areas in both the ventral and dorsal visual pathways that lie anterior and lateral to early retinotopic cortex. The parcellation of these areas is difficult because they are largely non-retinotopic [1] and different types of objects activate slightly different regions (Figure 1).

Whereas objects, houses and scenes (as compared with textures) activate both ventral and dorsal regions, faces and animals (as compared with textures) activate mainly lateral and ventral regions (Figure 1). Interestingly, faces and animals seem to activate similar regions, but houses and scenes activate different regions from those activated by faces and animals. These patterns of activation across ventral temporal cortex for certain object categories (e.g. faces [2–4; Figure 2, red], and houses [5–7; Figure 2, green]) are replicable within the same subject [8••,9•], and across subjects [10••,11•], and are invariant to the object's format. Other categories that have been reported to selectively activate focal regions of cortex selectively include animals [12,13], tools [12,13] and letter strings [11•,14].

Currently, the main debate is whether regions that elicit maximal response for a category should be treated as a module for the representation of that category, or whether they are part of a more general object recognition system [8••,9•,15••]. Furthermore, many of these object-selective regions also respond strongly to object fragments [16,17•], which further suggests that the underlying representation is not necessarily of whole objects.

Below I outline several approaches that attempt to explain the functional organization of the human ventral stream.

### Limited category-specific modules and a general area for all other subjects

Kanwisher and co-workers [3,5,18,19•] have suggested that ventral temporal cortex contains a limited number of modules specialized for the recognition of special categories such as faces (fusiform face area; FFA [3]), places (parahippocampal place area; PPA [5]) and body parts (extrastriate body part area; EBA [19•]). The remaining cortex, which shows little selectivity for particular object categories, is a general purpose mechanism

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Figure 1
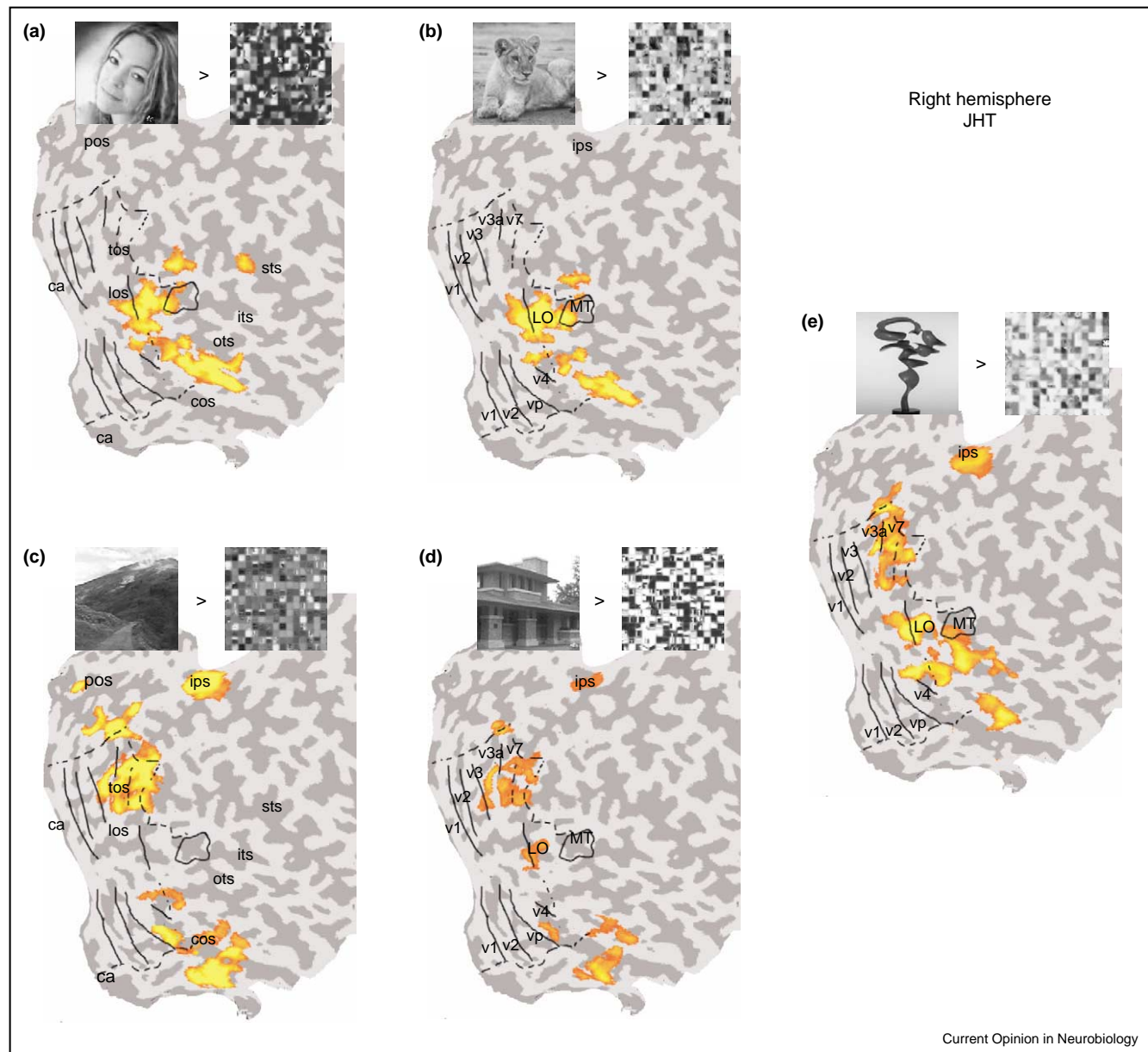
Different object categories activate different regions across the ventral and dorsal streams. Here we show areas that are activated more by objects than texture patterns. Textures were created by randomly scrambling object pictures into 400 squares. These maps were obtained in the same individual with the same threshold level and were highly significant at the voxel level ($P < 10^{-6}$). The color-coding indicates statistical significance. Data analysis was done with Brainvoyager (Brain Innovation, Masstricht, Netherlands) on a voxel-by-voxel basis (resolution $3 \times 3 \times 3$ mm). Comparison between objects and textures identifies both category-specific regions and nonspecific regions involved in representing many objects. Retinotopic visual areas were identified in separate scans in which we mapped both phase and eccentricity using complex visual stimuli [25]. **(a)** Areas showing higher activation in response to faces versus textures. These regions include the fusifom gyrus, the lateral occipital sulcus, the posterior part of middle temporal gyrus and a focus in the superior temporal sulcus. **(b)** Areas showing higher activation in response to four-legged mammals versus textures. Note that these regions are similar to regions that are activated when subjects view faces (excluding the superior temporal sulcus focus). Increasing the threshold level reduces the extent of the activated regions for both faces and animals, but the centers of the activated regions are similar. **(c)** Areas showing higher activation in response to scenes (which contain no obvious object) versus textures. Note that the pattern of activation is strikingly similar to regions activated by houses. In the ventral stream, areas that show higher activation for houses and scenes in the collateral sulcus consist of two foci: a posterior focus that partially overlaps with v4, and an anterior focus in the collateral sulcus/parahippocampal gyrus that prefers peripheral visual stimuli. **(d)** Areas showing higher activation in response to houses versus textures. Ventral regions include lateral occipital, regions in the medial bank of the collateral sulcus and the parahippocampal gyrus. Dorsal regions include v7 and an additional region lateral to v3a that is yet to be named. Note that these regions differ from the regions activated when people view faces or animals, with the exception of lateral occipital, which was activated by all categories. **(e)** Cortical regions showing higher activation in response to pictures of novel objects versus texture

Figure 2
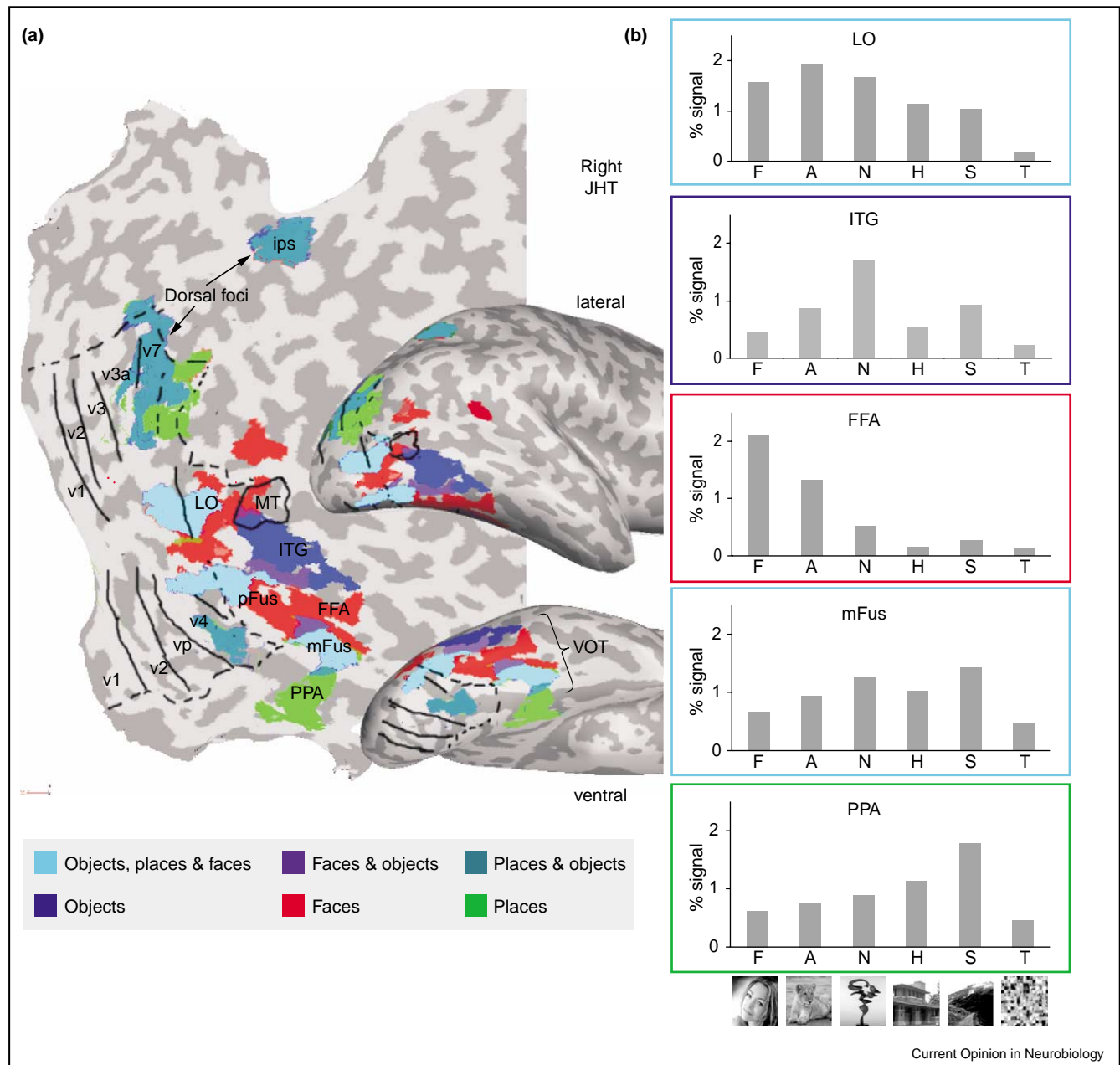
Object-selective regions in the human brain. **(a)** The maps shown in Figure 1 were combined into a single map, which is displayed on the flattened, lateral and ventral view of the right hemisphere. **(b)** Percentage change in the signal from several regions of interests (ROIs) of the same size (200 mm^3) centered on each ROI: LO, lateral occipital (Talairach coordinates [x,y,z]: 40,−74,−2); ITG, ROI centered on blue region in the inferior temporal gyrus (46,−58,−3); FFA, fusiform face area (40,−50,−15); PPA, parahippocampal place area (25,−35,−9); mFus, region in the mid fusiform that responds to all object categories (33,−38,−15); Pfus, posterior fusiform gyrus.

(Figure 1 Legend) patterns. Object-selective regions in the ventral stream consist of the lateral occipital complex (LOC), which can be subdivided to at least three partitions: lateral occipital (LO), which is located posterior to MT, a region in the inferior temporal gyrus and a region in the mid fusiform gyrus (mFus). In the dorsal stream, object-selective areas include v7, which lies anterior to v3a located in the posterior bank of the intraparietal sulcus and responds both to objects and scenes, and a region in the intraparietal sulcus that has a separate fovea and periphery organization. Abbreviations: CA, calcarine sulcus; COS, collateral sulcus; IPS, intraparietal sulcus; ITS, inferior temporal sulcus; MT, human motion area; OTS, occipito-temporal sulcus; STS, superior temporal sulcus; TOS, transverse occipital sulcus.

for perceiving any shape of any kind of visually presented object. This suggests that there is one region for general object recognition and a few modules for domain-specific processing.

Process maps

Tarr and Gauthier [20] have suggested that object representations are clustered according to the type of processing that is required, rather than according to their visual attributes. It is possible that different levels of processing may require dedicated computations that are initiated in localized cortical regions. For example, faces are usually recognized at the individual level, but objects are typically recognized at the category level. Following this reasoning, Gauthier and Tarr and their co-workers [21,22] have suggested that the FFA is not a region for face recognition, but rather a region for subordinate identification of any object category that is automated by expertise.

Topographic representation

Malach *et al.* [23] have suggested that cortical topography, in particular eccentricity mapping, underlies the organization of ventral [10••] and dorsal stream [24] object areas. They have shown that some object categories have specific eccentricity biases. For example, houses [10••,24] activate regions that contain peripheral visual field representations, whereas faces [10••,24] and letters [11•] activate regions that have a bias towards central representations. Malach *et al.* [23] propose that the organization of object selective regions is driven by resolution needs. Thus, objects for which recognition depends on an analysis of fine details will be associated with centrally biased representations, and objects for which recognition requires large-scale integration will be associated with peripherally biased representations.

Distributed object-form topography

Haxby *et al.* [8••] have proposed an 'object form topography' in which occipito-temporal cortex has a topographically organized representation of form attributes. The representation of an object is reflected by a distinct pattern of response across all ventral cortex, and this distributed activation produces the visual perception. Haxby *et al.* [8••] showed that the activation patterns for eight object categories were replicable, and that the response to a given category could be determined by the distributed pattern of activation across all VOT cortex. Notably, their analysis indicated that it is possible to predict the category of the object even when regions that show maximal activation to a particular category are excluded.

Recently, Spiridon and Kanwisher [9•] showed that these patterns are replicable even when the object format is changed and when objects are shown from a different viewpoint. However, their study showed that areas that elicit maximal activations for faces and places do not seem to be useful in discriminating between non-preferred categories.

Representation of objects in higher order areas

In the first section, I described the cortical regions that are activated when people look at objects. In this section, I discuss how objects are represented in the cortex. Any useful object recognition system should have 'perceptual constancy' — that is, it should be relatively insensitive to the precise physical cues that define an object.

Converging evidence suggests that object-selective regions in the ventral and dorsal stream show perceptual constancy under many manipulations: object-selective regions in the ventral stream areas are activated when subjects view objects defined only by luminance [25], texture [25,26], motion [25] or stereo [27] cues, but not when subjects view textures, stationary dots patterns, coherently moving dots or gratings defined by either motion or stereo. Other studies have shown that activation of object-selective areas is independent of object format (gray-scale or line drawings [28,29]) and these regions are also activated when subjects perceived simple shapes that are defined with illusory contours [30].

Several recent studies indicate that object-selective regions in the ventral stream represent shapes rather than contours. Kourtzi and Kanwisher [31••] have found that adaptation (indicative of a common neural representation [32•]) is observed when objects have the same shape but different contours, but not when contours are identical and the perceived shape is different. Similarly, Lerner *et al.* [33] have shown that different local contours that yield similar percepts (occluded versus non-occluded shapes) produce similar activation in object-selective regions, but similar local contours that yield different percepts (scrambled occluded versus occluded) produce different levels of activation in the same regions.

Another requirement for an object-recognition system is that it will be invariant to external viewing conditions that affect objects' appearance but not their identity. My colleagues and I [34] have previously shown, using fMR-adaptation [32•], that VOT (but not lateral occipital) regions exhibit some degree of invariance to objects' size and location. In contrast, we found that object representations in VOT are not invariant to object rotations around the vertical axis or the direction of illumination. These results suggest that object representations at the level of VOT are not viewpoint invariant representations. Recently, however, other researchers [35,36] have shown some degree of viewpoint invariance for object representations in VOT. One possibility is that the measured degree of sensitivity to object rotation depends on the magnitude of object rotation, which varied considerably between studies.

Taken together, these results demonstrate that within the same cortical regions there is invariance to a wide range of visual cues that generate object form and invariance to some object transformations. This provides strong evidence for the role of the occipito-temporal object areas in representing object shape.

The role of object-selective regions in object recognition

Although occipito-temporal object-selective regions are activated strongly when subjects view pictures of objects and have a large degree of perceptual constancy, this does not by itself prove that they are the loci in the brain that 'perform' object recognition. Activation during object viewing could be induced by other processes, such as visual attention, arousal, figure-ground segmentation and surface extraction among others. However, several recent studies show that activation in ventral (but not dorsal) object-selective areas is correlated to object perception rather than to low-level features in the visual stimulus [27,31••,37–44,45•,46,47,48•,49,50].

The correlation between perception and brain activation in lateral and ventral object areas has been demonstrated using various methods. Some researchers have monotonically varied a parameter that affects the ability of

Figure 3
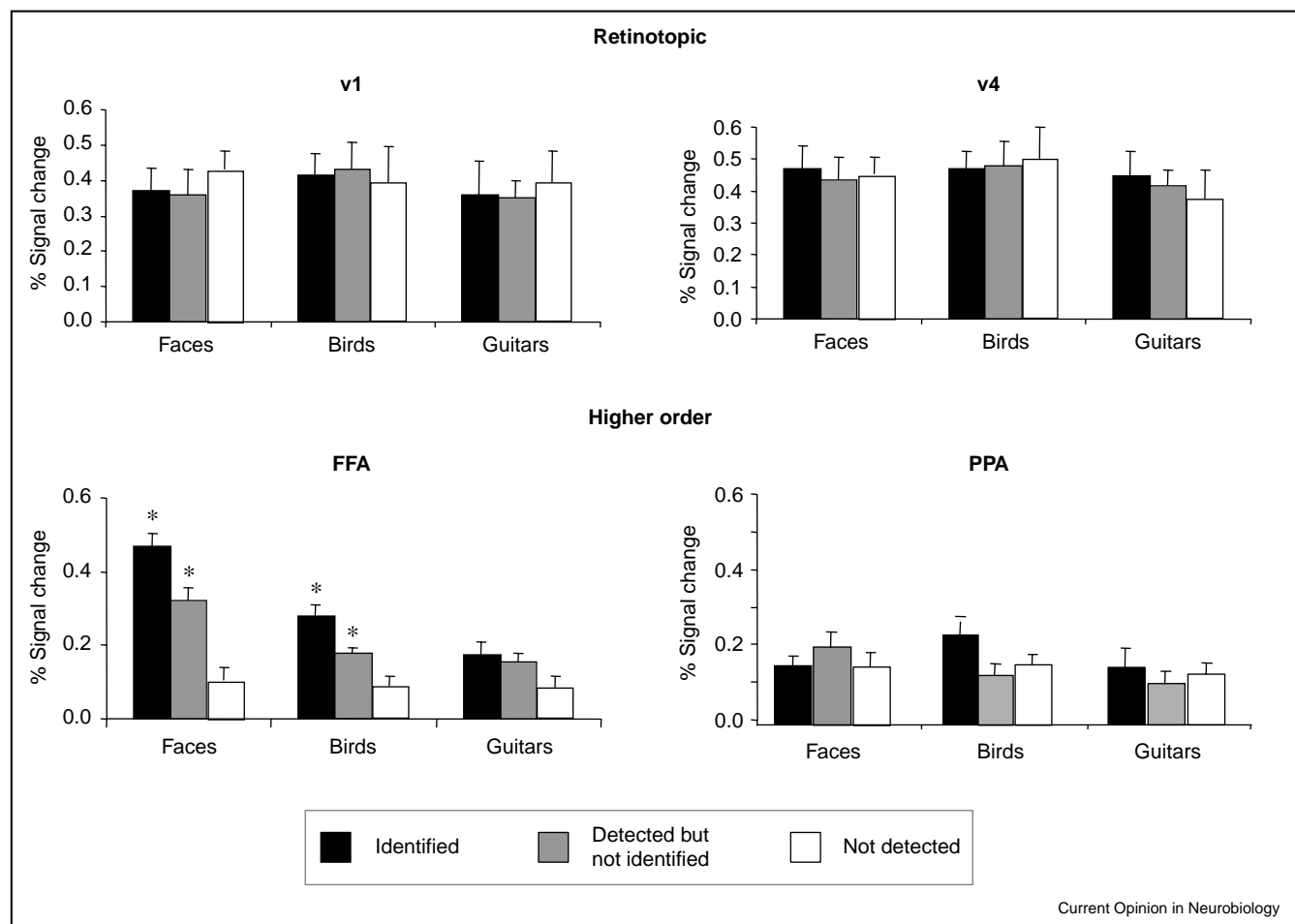
Activation of the ventral visual pathway as a function of success at object identification or object detection. Shown is the percentage change in the signal, taken from V1, V4, FFA and PPA, averaged across five subjects. In this experiment, subjects looked at pictures of objects that were presented for 33 or 50 ms (threshold was set individually for each subject) and then masked for 2 s. In separate runs, the subjects saw many pictures of faces, birds or guitars. A third of the trials included different pictures of a target subordinate category (e.g. pigeons), a third of the trials contained pictures of other objects from the same basic level (e.g. other birds) and a third of the trials were fixation trials. The trial order was counterbalanced. Subjects were required to respond to each picture according to whether they identified the subordinate category target (e.g. pigeon), they detected an object but could not identify it, or they could not detect an object at all (for details see Grill-Spector [51•]). Trials were sorted according to the recognition performance of the subjects. Here, data are shown from trials in which the target subordinate category was presented. Asterisks on identified trials indicate significantly higher signal versus trials in which objects were detected but not identified ($P < 0.01$). Asterisks on detected trials indicate significantly higher signal versus trials in which objects were present but not detected ($P < 0.01$). Retinotopic regions show no main effect of category or success at identification or detection. FFA shows a main effect of success and category. PPA shows no main effect of success.

subjects to recognize objects and have tracked the correlation between changes in brain activation and recognition performance of the subjects. Parameters that have been manipulated include image presentation duration [42], the amount of visible object behind occluding binds [43], object contrast [49], and the degree of coherence of letters [48•] and objects [43] presented in noise.

Such studies have shown that pre-recognition activation in object-selective regions is lower than recognition activation, and that activation increases monotonically until objects are recognized. In some of these studies, however, the visual stimulus was not identical in the pre-recognition and recognition conditions. Thus, an alternative interpretation is that the observed changes in brain activation were correlated to changes in the visual stimulus rather than an improvement in recognition performance.

Others have used bi-stable phenomena such as binocular rivalry [39,50], the Rubin face–vase illusion [46,47] and ambiguous figures [40] to track changes in brain activation that correlate with different perceptual states. The advantage of bi-stable phenomena is that the perception changes when the physical stimulus remains unchanged. These studies have shown that there is higher activation in face-selective regions in the fusiform gyrus when subjects perceive a face than when a face is not perceived.

A different approach is to show pictures close to a recognition threshold, and to compare brain activation in trials where subjects recognize objects to brain activation in trials where objects are present but not recognized [42,45•,51•]. Trials in which subjects correctly recognize objects produce a higher signal in lateral occipital and VOT areas than trials in which objects are present but not recognized. Indeed, using this approach we demonstrated [42] a correlation between subjects' object naming performance and activation in object-selective areas. Subjects initially could not recognize most of the objects when they were presented for brief exposures of 40 ms and then masked. By implicit training we improved subjects' recognition performance on these images. Post-training, when subjects were presented with the same images at the same exposure duration their performance increased by a factor of two. Importantly, when subjects were scanned when they performed this task, the fMRI signal from object-selective regions increased in correlation with the improvement in their recognition performance. An advantage of this design is that it can be used to tease apart processing stages involved in object recognition.

My colleagues and I [51•,52•] used this approach to test whether distinct areas across the human ventral stream were involved in different recognition tasks: detection without explicit recognition (object versus texture) or subordinate identification (e.g., pigeon versus bird) [51•]. We used a rapid event-related fMRI experiment, in which subjects viewed briefly presented objects that were immediately masked. Our data [51•] indicated that regions that were correlated with successful identification of a category were also correlated with successful detection of that category. In contrast, we found that different subregions across lateral and ventral occipito-temporal cortex were correlated with successful identification of different object categories [51•]. Notably, not all regions in the ventral stream were found to be correlated with successful recognition of a category. For example, FFA activation was correlated with successful identification and detection of faces and birds but not guitars (Figure 3, FFA), and PPA activation was not correlated with successful identification or detection of faces, birds or guitars (Figure 3, PPA). These data imply that successful recognition is initiated on a sparse distributed representation of objects across the ventral stream and not activation across the whole ventral cortex as suggested by Haxby and colleagues [8••].

In contrast to our findings that higher orders areas were correlated with success at object detection and identification, retinotopic visual areas in the human cortex were not correlated with success at object recognition (Figure 3, retinotopic). Taken together, these results suggest that activity in lateral occipital and VOT regions reflects the perceived object rather than the physical stimulus.

Conclusions

Neuroimaging studies have shown that several object-selective regions in the occipito-temporal cortex are involved in representing and perceiving objects and faces. These regions represent object shape rather than contours or other low-level features. In addition, higher activation in these regions occurs when subjects successfully recognize an object than when an object is present but not recognized. Future studies are required to elucidate the nature of object representations in the ventral visual pathway and the computational processes performed on these representations that facilitate this remarkable human ability.

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- •• of outstanding interest

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In this study we used rapid event-related fMRI experiments, in which we limited subjects' ability to recognize objects by presenting pictures briefly and then masking them. We searched for brain regions that were correlated with subjects' success at detecting or identifying objects. Our results provide evidence that similar regions across the ventral stream are correlated with object detection and identification, but different subregions are correlated with the recognition of different object categories.

52. Liu J, Harris A, Kanwisher N: **Stages of processing in face**
• **perception: an MEG study**. *Nat Neurosci* 2002, **5**:910-916.
The authors use magnetoencephalography to study processing stages in face perception. They show that an early component (M100) that occurs 100 ms after stimulus onset over extrastriate cortex is correlated with successful face detection, whereas a later component (M170) that occurs 170 ms after stimulus onset is correlated with face identification.