

# What Has fMRI Taught Us About Object Recognition?

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## 6.1 Introduction

Humans can effortlessly recognize objects in a fraction of a second despite large variability in the appearance of objects (Thorpe et al. 1996). What are the underlying representations and computations that enable this remarkable human ability? One way to answer these questions is to investigate the neural mechanisms of object recognition in the human brain. With the advent of functional magnetic resonance imaging (fMRI) about 15 years ago, neuroscientists and psychologists began to examine the neural bases of object recognition in humans. Functional magnetic resonance imaging (fMRI) is an attractive method because it is a noninvasive technique that allows multiple measurements of brain activation in the same awake behaving human. Among noninvasive techniques, it provides the best spatial resolution currently available, enabling us to localize cortical activations in the spatial resolution of millimeters (as fine as 1 mm) and at a reasonable time scale (in the order of seconds).

Before the advent of fMRI, knowledge about the function of the ventral stream was based on single-unit electrophysiology measurements in monkeys and on lesion studies. These studies showed that neurons in the monkey inferotemporal (IT) cortex respond to shapes (Fujita et al. 1992) and complex objects such as faces (Desimone et al. 1984), and that lesions to the ventral stream can produce specific deficits in object recognition, such as agnosia (inability to recognize objects) and prosopagnosia (inability to recognize faces, Farah 1995). However, interpreting lesion data is complicated because lesions are typically diffuse (usually more than one region is damaged), typically disrupt both a cortical region and its connectivity, and are not replicable across patients. Therefore, the primary knowledge gained from fMRI research was which cortical sites in the normal human brain are involved in object recognition. The first set of fMRI studies of object and face recognition in humans identified the regions in the human brain that respond selectively to objects and faces (Malach et al. 1995; Kanwisher et al. 1997; Grill-Spector et al. 1998b). Then a series of studies demonstrated that activation in object- and face-selective regions correlates with success at recognizing object and faces, respectively, providing striking evidence for the involvement of these regions in

recognition (Grill-Spector et al. 2000; Bar et al. 2001; Grill-Spector et al. 2004). Once researchers found which regions in the cortex are involved in object recognition, the focus of research shifted to examining the nature of representations and computations that are implemented in these regions to understand how they enable efficient object recognition in humans.

In this chapter I will review fMRI research that provided important knowledge about the nature of object representations in the human brain. I chose to focus on this topic because results from these experiments provide important insights that can be used by computer scientists when they design artificial object recognition systems. For example, one of the fundamental problems in recognition is how to recognize an object across variations in its appearance (invariant object recognition). Understanding how a biological system has solved this problem may give clues for how to build a robust artificial recognition system. Further, fMRI is more adequate for measuring object representations than the temporal sequence of computations en route to object recognition because the time scale of fMRI measurements is longer than the time scale of the recognition process (the temporal resolution of fMRI is in the order of seconds, whereas object recognition takes about 100–250 ms). Nevertheless, combining psychophysics with fMRI may give us some clues about what kind of visual processing is implemented in distinct cortical regions. For example, finding regions whose activation is correlated with success at some tasks, but not others, may suggest the involvement of particular cortical regions in one computation, but not another.

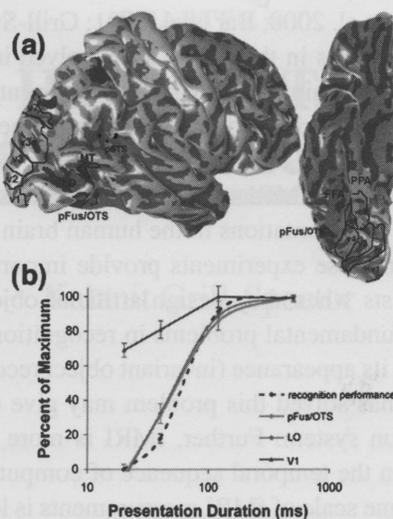
In discussing how fMRI has impacted our current understanding of object representations, I will focus on results pertaining to two aspects of object representation:

- How do the underlying representations provide for invariant object recognition?
- How is category information represented in the ventral stream?

I have chosen these topics because (i) they are central topics in object recognition for which fMRI has substantially advanced our understanding, (ii) Some findings related to these topics stirred considerable debate (see sect. 6.7), and (iii) some of the fMRI findings in humans are surprising given prior knowledge from single-unit electrophysiology in monkeys. In organizing the chapter, I will begin with a brief introduction of the functional organization of the human ventral stream and a definition of object-selective cortex. Then I will describe research that elucidated the properties of these regions with respect to basic coding principles. I will continue with findings related to invariant object recognition, and end with research and theories regarding category representation and specialization in the human ventral stream.

## 6.2 The Functional Organization of the Human Ventral Stream

The first set of fMRI studies on object and face recognition in humans was devoted to identifying the regions in the brain that are object- and face-selective. Electrophysiology research in monkeys suggested that neurons in higher-level regions respond to shapes and objects more than simple stimuli such as lines, edges, and patterns (Desimone et al. 1984; Fujita et al. 1992; Logothetis et al. 1995). Based on these findings, fMRI studies measured brain activation when people viewed pictures of objects compared to



**Figure 6.1.** Object-, face-, and place-selective cortex. (a) Data of one representative subject shown on her partially inflated right hemisphere: lateral view (*left*); ventral view (*right*). *Dark gray* indicates sulci. *Light gray* indicates gyri. *Black lines* delineate retinotopic regions. *Blue regions* delineate object-selective regions (objects > scrambled objects), including LO and pFus/OTS ventrally as well as dorsal foci along the intraparietal sulcus (IPS). *Red regions* delineate face-selective regions (faces > non-faces objects), including the FFA, a region in LOS and a region in posterior STS. *Magenta regions* delineate overlap between face- and object-selective regions. *Green regions* delineate place-selective regions (places > objects), including the PPA and a dorsal region lateral to the IPS. *Dark green regions* delineate overlap between place- and object-selective regions. All maps thresholded at  $P < 0.001$ , voxel level. (b) LO and pFus/OTS (but not V1) responses are correlated with recognition performance (Grill-Spector et al. 2000). To superimpose recognition performance and fMRI signals on the same plot, all values were normalized relative to the maximum response for the 500-ms duration stimulus.

For fMRI signals (blue, red, and orange lines) =  $\frac{\% \text{ signal}(\text{condition})}{\% \text{ signal}(500 \text{ ms})}$ . For recognition performance (black) =  $\frac{\% \text{ correct}(\text{condition})}{\% \text{ correct}(500 \text{ ms})}$ . (See color plate 6.1.)

scrambled objects (have the same local information and statistics, but do not contain an object) or texture patterns (e.g., checkerboards, which are robust visual stimuli, but do not elicit a percept of a global form). These studies found a constellation of regions in the lateral occipital cortex (or the lateral occipital complex, LOC), beginning around the lateral occipital sulcus, posterior to MT, and extending ventrally into the occipitotemporal sulcus (OTS) and the fusiform gyrus (Fus), that respond more to objects than controls. The LOC is located lateral and anterior to early visual areas (V1–V4), (Grill-Spector et al. 1998a; Grill-Spector et al. 1998b) and is typically divided into two subregions: LO, a region in the lateral occipital cortex, adjacent and posterior to MT; and pFus/OTS; a ventral region overlapping the OTS and posterior fusiform gyrus (Fig. 6.1).

The lateral occipital complex (LOC) responds similarly to many kinds of objects and object categories (including novel objects) and is thought to be in the intermediate- or high-level stages of the visual hierarchy. Importantly, LOC activations are correlated with subjects' object recognition performance. High LOC responses correlate with

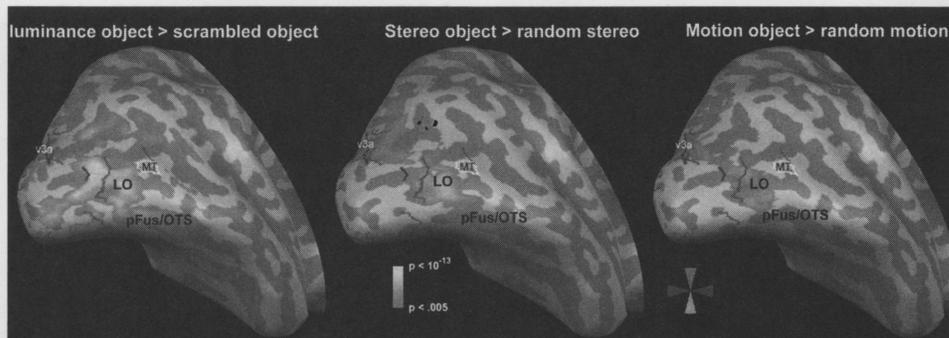
successful object recognition (hits), and low LOC responses correlate with trials in which objects are present but not recognized (misses) (Fig. 6.1(b)). Object-selective regions are also found in the dorsal stream (Grill-Spector 2003; Grill-Spector and Malach 2004), but activation of these regions does not correlate with object recognition performance (Fang and He 2005). These regions may be involved in computations related to visually guided actions toward objects (Culham et al. 2003). However, a comprehensive discussion of the role of the dorsal stream in object perception is beyond the scope of this chapter.

In addition to the LOC, researchers found several ventral regions that show preferential responses to specific object categories. The search for regions with categorical preference was motivated by reports that suggested that lesions to the ventral stream can produce very specific deficits, such as the inability to recognize faces or the inability to read words, while other visual (and recognition) faculties remain preserved. By contrasting activations to different kinds of objects, researchers found ventral regions that show higher responses to specific object categories: including lateral fusiform regions that respond more to animals than tools, and medial fusiform regions that respond to tools more than animals (Martin et al. 1996; Chao et al. 1999), a region in the left OTS that responds more strongly to letters than textures (the visual word form area, or VWFA) (Cohen et al. 2000); several foci that respond more strongly to faces than to other objects (Kanwisher et al. 1997; Haxby et al. 2000; Hoffman and Haxby 2000; Grill-Spector et al. 2004), including the well known fusiform face area (FFA) (Kanwisher et al. 1997), regions that respond more strongly to houses and places than faces and objects (including a region in the parahippocampal gyrus, the parahippocampal place area (PPA) (Epstein and Kanwisher 1998); regions that respond more strongly to body parts than faces and objects, including a region near MT called the extrastriate body area (EBA) (Downing et al. 2001); and a region in the fusiform gyrus (the fusiform body area, or FBA) (Schwarzlose et al. 2005)). Nevertheless, many of these object-selective and category-selective regions respond to more than one object category and also respond strongly to object fragments (Grill-Spector et al. 1998b; Lerner et al. 2001; Lerner et al. 2008). This suggests that one must be cautious when interpreting the nature of the selective responses. It is possible that the underlying representation is perhaps of object parts, features, and/or fragments and not of whole objects or object categories.

Findings of category-selective regions in the human brain initiated a fierce debate about the principles of functional organization in the ventral stream. Are there regions in the cortex that are specialized for any object category? How abstract is the information represented in these regions (e.g., is category information represented in these regions, or low-level visual features that are associated with categories)? I will address these questions in detail in section 6.7.

### 6.3 Cue-Invariant Responses in the LOC

Although findings of object-selective responses in the human brain were suggestive of the involvement of these region in processing objects, there are many differences between objects and scrambled objects (or objects and texture patterns). Objects have

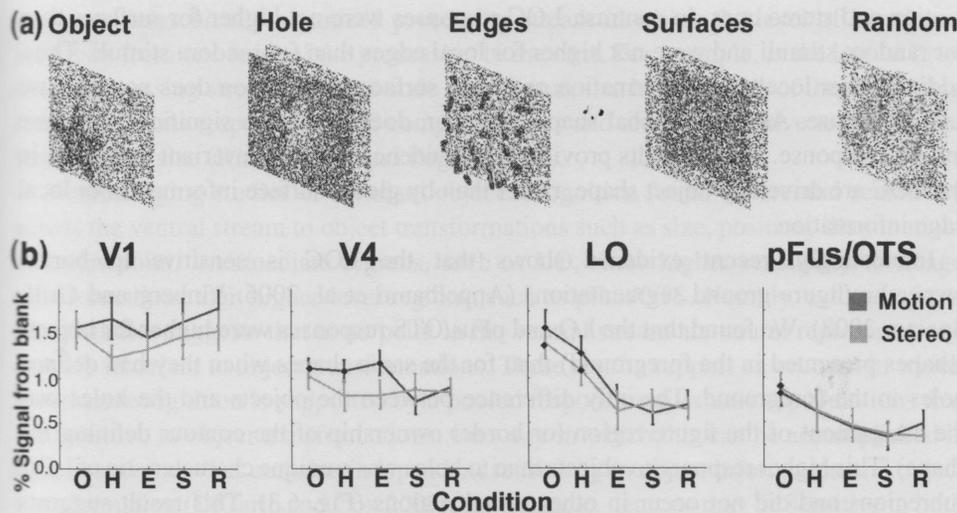


**Figure 6.2.** Selective responses to objects across multiple visual cues across the LOC. Statistical maps of selective response to object from luminance, stereo and motion information in a representative subject. All maps were thresholded at  $P < 0.005$ , voxel level, and are shown on the inflated right hemisphere of a representative subject. (a) Luminance objects > scrambled objects. (b) Objects generated from random dot stereograms versus structureless random dot stereograms (perceived as a cloud of dots). (c) Objects generated from dot motion versus the same dots moving randomly. Visual meridians are represented by *red* (upper), *blue* (horizontal), and *green* (lower) lines. *White contour* indicates a motion-selective region, or MT. Adapted from Vinberg and Grill-Spector 2008. (See color plate 6.2.)

shapes, surfaces, and contours; they are associated with a meaning and semantic information; and they are generally more interesting than texture patterns. Each of these factors may affect the higher fMRI response to objects than controls. Differences in low-level visual properties across objects and controls may be driving some of these effects as well.

Converging evidence from several studies revealed an important aspect of coding in the LOC: it responds to object shape, not low-level visual features. Several studies showed that all LOC subregions (LO and pFus/OTS) are activated more strongly when subjects view objects independent of the type of visual information that defines the object form (Grill-Spector et al. 1998a; Kastner et al. 2000; Kourtzi and Kanwisher 2000, 2001; Gilaie-Dotan et al. 2002; Vinberg and Grill-Spector 2008) (Fig. 6.2). The lateral occipital complex (LOC) responds more strongly to (1) objects defined by luminance than to luminance textures; (2) objects generated from random dot stereograms than to structureless random dot stereograms; (3) objects generated from structure from motion than to random (structureless) motion; and (4) objects generated from textures than to texture patterns. The response of the LOC to objects is also similar across object format<sup>1</sup> (gray-scale, line drawings, and silhouettes), and it responds to objects delineated by both real and illusory contours (Mendola et al. 1999; Stanley and Rubin 2003). Kourtzi and Kanwisher (Kourtzi and Kanwisher 2001) also showed that there was fMRI-adaptation (fMRI-A, indicating a common neural substrate), when objects had the same shape but different contours, but that there was no fMRI-A when the shared contours were identical but the perceived shape was different, suggesting that the LOC responds to global shape rather than to local contours (see also Lerner et al. 2002; Kourtzi et al. 2003). Overall, these studies provided fundamental knowledge

<sup>1</sup> Selective responses to faces and houses across stimulus format (photographs, line drawings, and silhouettes) have also been shown for the FFA and PPA, respectively.



**Figure 6.3.** Responses to shape, edges, and surfaces across the ventral stream. (a) Schematic illustration of experimental conditions. Stimuli were generated from either motion or stereo information alone and had no luminance edges or surfaces (except for the screen border, which was present during the entire experiment, including blank baseline blocks). For illustration purposes, darker regions indicate front surfaces. From left to right: *Object* on the front surface in front of a flat background plane. *Hole* on the front surface in front of a flat background. *Edges* were generated by scrambling the shape contours. *Surfaces*, Two semitransparent flat surfaces at different depths. *Random* stimuli with no coherent structure, edges, global surfaces, or global shape. Random stimuli had the same relative disparity or depth range as other conditions. See examples of stimuli: <http://www-psych.stanford.edu/~kalanit/jnpstim/>. (b) Responses to objects, holes, edges, and global surfaces across the visual ventral-processing hierarchy. Responses: mean  $\pm$  SEM across eight subjects. O, object; H, hole; S, surfaces; E, edges; R, random; diamonds, significantly different than random at  $P < 0.05$ . Adapted from Vinberg and Grill-Spector 2008.

by showing that activation of the LOC is driven by shape rather than by the low-level visual information that generates form.

In a recent study, we examined whether the LOC response to objects is driven by their global shape or their surface information and whether LOC subregions are sensitive to border ownership. One open question in object recognition is whether the region in the image that belongs to the object is first segmented from the rest of the image (figure-ground segmentation) and then recognized, or whether knowing the shape of an object aids its segmentation (Peterson and Gibson 1994b, 1994a; Nakayama et al. 1995). To address these questions, we scanned subjects when they viewed stimuli that were matched for their low-level information and generated different percepts: (1) a percept of an object in front of a background object, (2) a shaped hole (same shape as the object) in front of a background, (3) two flat surfaces without shapes, (4) local edges (created by scrambling the object contour) in front of a background, or (5) random dot stimuli with no structure (Fig. 6.3(a)) (Vinberg and Grill-Spector 2008). We repeated the experiment twice, once with random dots that were presented stereoscopically and once with random dots that moved. We found that LOC responses (both LO and pFus/OTS) were higher for objects and shaped holes than for surfaces, local edges, or random stimuli (Fig. 6.3(b)). These results were observed for both

motion and stereo cues. In contrast, LOC responses were not higher for surfaces than for random stimuli and were not higher for local edges than for random stimuli. Thus, adding either local edge information or global surface information does not increase LOC response. Adding a global shape, however, does produce a significant increase in LOC response. These results provide clear evidence that cue-invariant responses in the LOC are driven by object shape, rather than by global surface information or local edge information.

Interestingly, recent evidence shows that the LOC is sensitive to border ownership/figure-ground segmentation) (Appelbaum et al. 2006; Vinberg and Grill-Spector 2008). We found that the LO and pFus/OTS responses were higher for objects (shapes presented in the foreground) than for the same shapes when they had defined holes in the foreground. The only difference between the objects and the holes was the assignment of the figure region (or border ownership of the contour defining the shape). This higher response to objects than to holes was a unique characteristic of LOC subregions and did not occur in other visual regions (Fig. 6.3). This result suggests that the LOC prefers shapes (and contours) when they define the figure region. One implication of this result is that the same brain machinery may be involved in both recognizing objects and in determining which region in the visual input contains the figure region. Thus, one consideration for computer scientists is that an effective object recognition algorithm should determine both what is the the object in the scene as well as which region in the scene corresponds to the object.

#### 6.4 Neural Bases of Invariant Object Recognition

The literature reviewed so far provides evidence that the LOC is involved in the recognition and processing of object form. Given the LOC's role in object perception, one may consider, how it deals with variability in an object's appearance. Many factors can affect the appearance of objects. Changes in an object's appearance can occur as a result of the object being at different locations relative to the observer, which will affect its retinal projection of objects in terms of size and position. Also, the 2-D projection of a 3-D object on the retina varies considerably owing to changes in its rotation and viewpoint relative to the observer. Other changes in appearance occur because of differential illumination conditions, which affect an object's color, contrast, and shadowing. Nevertheless, humans are able to recognize objects across large changes in their appearance, which is referred to as *invariant object recognition*.

A central topic of research in the study of object recognition is understanding how invariant recognition is accomplished. One view suggests that invariant object recognition is accomplished because the underlying neural representations are invariant to the appearance of objects. Thus, this view suggests that there neural responses will remain similar even when the appearance of an object changes considerably. One means by which this can be achieved is by extracting from the visual input features or fundamental elements (such as geons (Biederman 1987) that are relatively insensitive to changes in objects' appearance. According to one influential model (recognition by components, or RBC; Biederman 1987), objects are represented by a library of geons, which are easy to detect in many viewing conditions, and by their spatial relations. Other theories suggest that invariance may be generated through a sequence of computations

across a hierarchically organized processing stream in which the level of invariance increases from one level of the processing to the next. For example, at the lowest level of the processing stream, neurons code local features; at higher levels of the processing stream, neurons respond to more complex shapes and are less sensitive to changes in position and size (Riesenhuber and Poggio 1999).

Neuroimaging studies of invariant object recognition found differential sensitivity across the ventral stream to object transformations such as size, position, illumination, and viewpoint. Intermediate regions, such as LO, show higher sensitivity to image transformations than higher-level regions, such as pFus/OTS. Notably, evidence from many studies suggests that at no point in the ventral stream are neural representations *entirely* invariant to object transformations. These results support an account in which invariant recognition is supported by a pooled response across neural populations that are sensitive to object transformations. One way in which this can be accomplished is by a neural code that contains independent sensitivity to object information and object transformation (DiCarlo and Cox 2007); for example, neurons may be sensitive to both object category and object position. As long as the categorical preference is retained across object transformations, invariant object information can be extracted.

### 6.5 Object and Position Information in the LOC

One variation that the object recognition system needs to deal with is variation in the size and position of objects. Size and position invariance are thought to be accomplished in part by an increase in the size of neural receptive fields along the visual hierarchy (i.e., as one ascends the visual hierarchy, neurons respond to stimuli across a larger part of the visual field). At the same time, a more complex visual stimulus is necessary to elicit significant responses in neurons (e.g., shapes instead of oriented lines). Findings from electrophysiology suggest that even at the highest stages of the visual hierarchy, neurons retain some sensitivity to object location and size although electrophysiology reports vary significantly about the degree of position sensitivity of IT neurons (Op De Beeck and Vogels 2000; Rolls 2000; DiCarlo and Maunsell 2003). A related issue is whether position sensitivity of neurons in higher visual areas manifests as an orderly, topographic representation of the visual field. Researchers have examined position and size sensitivity in the LOC and nearby cortex (such as PPA and FFA) using measurements of the mean response across a region of interest; fMRI-A, in which they measured sensitivity to changes in object size or position; and examination of the distributed response across the ventral stream to the same object or object category across sizes and positions.

Several studies documented sensitivity to both eccentricity and polar angle in distinct ventral stream regions. Both object-selective and category-selective regions in the ventral stream respond to objects presented at multiple positions and sizes. However, the amplitude of response to object varies across different retinal positions. The LO and pFus/OTS as well as category-selective regions (e.g., FFA, PPA) respond more strongly to objects presented in the contralateral versus ipsilateral visual field (Grill-Spector et al. 1998b; Hemond et al. 2007; McKyton and Zohary 2007). Some regions (LO and EBA) also respond more strongly to objects presented in the lower visual field (Sayres and Grill-Spector 2008; Schwarzlose et al. 2008). Responses also vary with

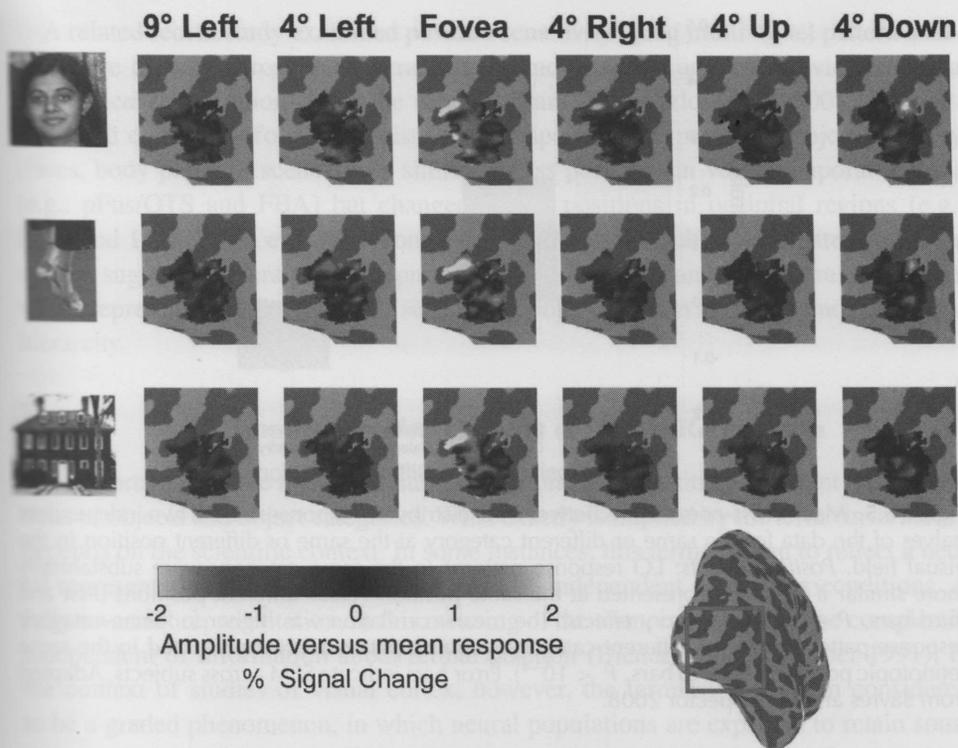
eccentricity: LO, FFA, and the VWFA respond more strongly to centrally presented stimuli, and the PPA responds more strongly to peripherally presented stimuli (Levy et al., 2001; Hasson et al. 2002; Hasson et al. 2003; Sayres and Grill-Spector 2008).

Using fMRI-A, my colleagues and I have shown that pFus/OTS, but not LO, exhibits some degree of insensitivity to an object's size and position (Grill-Spector et al. 1999). The fMRI-A method allows one to characterize the sensitivity of neural representations to stimulus transformations at a subvoxel resolution. fMRI-A is based on findings from single-unit electrophysiology that show that when objects repeat, there is a stimulus-specific decrease in the response of IT cells to the repeated image but not to other object images (Miller et al. 1991; Sawamura et al. 2006). Similarly, fMRI signals in higher visual regions show a stimulus-specific reduction (fMRI-A) in response to repetition of identical object images (Grill-Spector et al. 1999; Grill-Spector and Malach 2001; Grill-Spector et al. 2006a). We showed that fMRI-A can be used to test the sensitivity of neural responses to object transformation by adapting cortex with a repeated presentation of an identical stimulus and then examining adaptation effects when the stimulus is changed along an object transformation (e.g., changing its position). If the response remains adapted, it indicates that neurons are insensitive to the change; however, if responses return to the initial level (recover from adaptation), it indicates sensitivity to the change (Grill-Spector and Malach 2001).

Using fMRI-A we found that repeated presentation of the same face or object at the same position and size produces reduced fMRI activation or fMRI-A. This is thought to reflect stimulus-specific neural adaptation. Presenting the same face or object in different positions in the visual field or at different sizes also produces fMRI-A in pFus/OTS and FFA, indicating insensitivity to object size and position (Grill-Spector et al. 1999; see also Vuilleumier et al. 2002). This result is consistent with electrophysiology findings that showed that IT neurons that respond similarly to stimuli at different positions in the visual field also show adaptation when the same object is shown in different positions (Lueschow et al. 1994). In contrast, LO recovers from fMRI-A to images of the same face or object when presented at different sizes or positions. This indicates that LO is sensitive to object position and size.

Recently, several groups examined the sensitivity of the distributed response across the visual stream to object category and object position (Sayres and Grill-Spector 2008; Schwarzlose et al. 2008) and also object identity and object position (Eger et al. 2008). These studies used multi-voxel pattern analyses and classifier methods developed in machine learning to examine what information is present in the distributed responses across voxels in a cortical region. The distributed response can carry different information from the mean response of a region of interest when there is variation across voxels' responses.

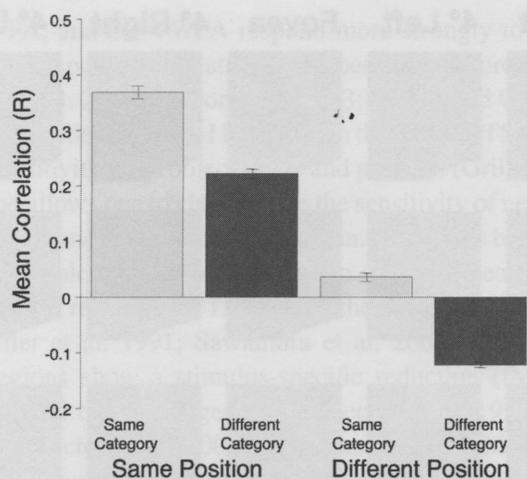
In order to examine sensitivity to position information, several studies examined whether distributed response patterns to same object category (or object exemplar) is the same (or different) when the same stimulus is presented in a different position in the visual field. In multi-voxel pattern analyses researchers typically split the data into two independent sets and examine the cross-correlation between the distributed responses to the same (or different) stimulus in the same (or different) position across the two datasets. This gives a measure of the sensitivity of distributed responses to object information and position. If responses are position-invariant, there will be a



**Figure 6.4.** LO distributed response patterns to different object categories and stimulus positions. Data are shown on the lateral aspect of the right hemisphere cortical surface for a representative subject. Each panel shows the distributed LO fMRI amplitudes after subtracting from each voxel its mean response. *Red and yellow*, Responses that are higher than the voxel's mean response. *Blue and cyan*, Responses that are lower than the voxel's mean response. *Inset*, Inflated right cortical hemisphere, with red square indicating the zoomed region. Note that pattern changes significantly across columns (positions) and to a lesser extent across rows (categories). Adapted from Sayres and Grill-Spector 2008. (See color plate 6.4.)

high correlation between the distributed responses to the same object category (or exemplar) at different positions. If responses are sensitive to position, there will be a low correlation between responses to the same object category (or exemplar) at different positions.

Figure 6.4 illustrates distributed LO responses to three categories: houses, limbs, and faces at six visual locations (fovea; 4° up, right, down, or left from the fovea; 9° left of fovea). Activation patterns for the same object category presented at different positions vary considerably (compare the response patterns in the same row across the different columns in Fig. 6.4). There is also variation (but to a lesser extent) across different object categories when presented at the same retinal position (same column, different rows, in Fig. 6.4). Surprisingly, position effects in LO were larger than category effects – that is, showing objects from the same category, but at a different position, reduced the correlation between activation patterns (Fig. 6.5, first vs. third bars) more significantly than changing the object category in the same position (Fig. 6.5, first vs. second bar). Importantly, position and category effects were independent, as there were no significant interactions between position and category



**Figure 6.5.** Mean cross-correlations between LO distributed responses across two independent halves of the data for the same or different category at the same or different position in the visual field. *Position effects:* LO response patterns to the same category were substantially more similar if they were presented at the same position versus different positions (first and third bars,  $P < 10^{-7}$ ). *Category effects:* The mean correlation was higher for same-category response patterns than for different-category response patterns when presented in the same retinotopic position (first two bars,  $P < 10^{-4}$ ). Error bars indicate SEM across subjects. Adapted from Sayres and Grill-Spector 2008.

(all  $F$  values  $< 1.02$ , all  $P$  values  $> 0.31$ ). Thus, changing both object category and position produced maximal decorrelation between distributed responses (Fig. 6.5, fourth bar).

We also examined whether position sensitivity in LO is manifested as an orderly topographic map (similar to retinotopic organization in lower visual areas), by measuring retinotopic maps in LO using standard traveling wave paradigms (Wandell 1999; Sayres and Grill-Spector 2008). We found a continuous mapping of the visual field in LO both in terms of eccentricity and polar angle. This topographic map contained an over-representation of the contralateral and lower visual field (more voxels preferred these visual field positions than the ipsilateral and upper visual fields). Although we did not consistently find a single visual field map (a single hemifield or quarterfield representation) in LO, this analysis suggests that there is preserved retinotopic information in LO that may underlie the position effects observed in analyses of distributed LO responses.

Overall, our data show that different object categories produce relatively small changes to both the mean and distributed response across LO (categorical effects are larger in the fusiform and parahippocampal gyri). In comparison, a modest  $4^\circ$  change in an object's position produces signal changes in LO that are as large or larger than the category modulation. This  $4^\circ$  displacement is well within the range for which humans can categorize and detect objects (Thorpe et al. 2001). This indicates a difference between the position sensitivity of recognition behavior and that of neural populations in LO. However, it is possible that performance in recognition tasks that require fine-grain discrimination between exemplars is more position sensitive, and limited by the degree of position sensitivity in LO.

A related recent analysis more broadly hierarchical organization (faces, body parts (e.g., pFus/OTS EBA and LO). These studies suggest which represent hierarchy.

It is important to note that the representation of objects depends on the spatial representation, which is fully invariant to the context of the object. It is to be a graded degree of sensitivity to stimulus selectivity (Rolls and growing literature distributed neural (Dill and Edelman maintaining some maintain information and Intra object-based (and Grill-Spector structural encoding robust way for model, object population of for fast decision to determine (2007). Finally, organization and where it is).

Another source of change across

A related recent study examined position sensitivity using multi-voxel pattern analysis more broadly across the ventral stream and provided additional evidence for a hierarchical organization across the ventral stream (Schwarzlose et al. 2008). Schwarzlose and colleagues found that distributed responses to a particular object category (faces, body parts, or scenes) was similar across positions in ventrotemporal regions (e.g., pFus/OTS and FBA) but changed across positions in occipital regions (e.g., EBA and LO). Thus, evidence from both fMRI-A and multi-voxel pattern analysis studies suggests a hierarchy of representations in the human ventral stream through which representations become less sensitive to object position as one ascends the visual hierarchy.

### 6.5.1 Implications for Theories of Object Recognition

It is important to relate imaging results to the concept of position-invariant representations of objects and object categories. What exactly is implied by the term "invariance" depends on the scientific context. In some instances, this term is taken to reflect a neural representation that is abstracted so as to be independent of viewing conditions. A fully invariant representation, in this meaning of the term, is expected to be completely independent of information about retinal position (Biederman and Cooper 1991). In the context of studies of visual cortex, however, the term is more often considered to be a graded phenomenon, in which neural populations are expected to retain some degree of sensitivity to visual transformations (like position changes) but in which stimulus *selectivity* is preserved across these transformations (Kobatake and Tanaka 1994; Rolls and Milward 2000; DiCarlo and Cox 2007). In support of this view, a growing literature suggests that maintaining local position information within a distributed neural representation may actually aid invariant recognition in several ways (Dill and Edelman 2001; DiCarlo and Cox 2007; Sayres and Grill-Spector 2008). First, maintaining separable information about position and category may also allow on to maintain information about the structural relationships between object parts (Edelman and Intrator 2000). Indeed some experiments suggest that LO may contain both object-based (McKyton and Zohary 2007) and retinal-based reference frames (Sayres and Grill-Spector 2008). The object-based reference frame may provide a basis for structural encoding. Second, separable position and object information may provide a robust way for generating position invariance by using a population code. Under this model, objects are represented as manifolds in a high-dimensional space spanned by a population of neurons. The separability of position and object information may allow for fast decisions based on linear computations (e.g., linear discriminant functions) to determine the object identity (or category) across positions see (DiCarlo and Cox 2007). Finally, separable object and position information may allow concurrent localization and recognition of objects (i.e., recognizing what the object is and determining where it is).

### 6.6 Evidence for Viewpoint Sensitivity Across the LOC

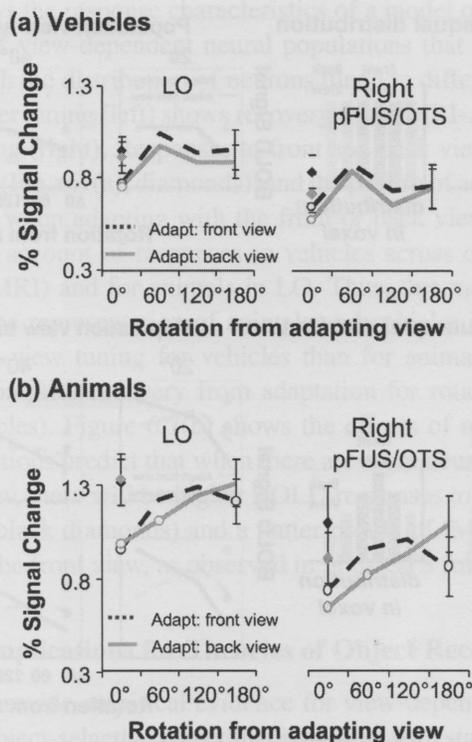
Another source of change in object appearance that merits separate consideration is change across rotation in depth. In contrast to position or size changes, in which

invariance may be achieved by a linear transformation, the shape of objects changes with depth rotation. This is because the visual system receives 2-D retinal projections of 3-D objects. Some theories suggest that view-invariant recognition across object rotations is accomplished by largely view-invariant representations of objects (generalized cylinders', Marr 1980; recognition by components', or RBC', Biederman 1987); that is, the underlying neural representations respond similarly to an object across its views. Other theories, however, suggest that object representations are view-dependent, that is, they consist of several 2-D views of an object (Ullman 1989; Poggio and Edelman 1990; Bulthoff and Edelman, 1992; Edelman and Bulthoff 1992; Bulthoff et al. 1995; Tarr and Bulthoff 1995). Invariant object recognition is accomplished by interpolation across these views (Ullman 1989; Poggio and Edelman 1990; Logothetis et al. 1995) or by a distributed neural code across view-tuned neurons (Perrett et al. 1998).

Single-unit electrophysiology studies in primates indicate that the majority of neurons in monkey inferotemporal cortex are view-dependent (Desimone et al. 1984; Logothetis et al. 1995; Perrett 1996; Wang et al. 1996; Vogels and Biederman 2002) with a small minority (5–10%) of neurons showing view-invariant responses across object rotations (Logothetis et al. 1995; Booth and Rolls 1998).

In humans, results vary considerably. Short-lagged fMRI-A experiments, in which the test stimulus is presented immediately after the adapting stimulus (Grill-Spector et al. 2006a), suggest that object representations in the LOC are view-dependent (Fang et al. 2007; Gauthier et al. 2002; Grill-Spector et al. 1999; but see Valyear et al. 2006). However, long-lagged fMRI-A experiments, in which many intervening stimuli occur between the test and adapting stimulus (Grill-Spector et al. 2006a), have provided some evidence for view-invariant representations in ventral LOC, especially in the left hemisphere (James et al. 2002; Vuilleumier et al. 2002) and the PPA (Epstein et al. 2008). Also, a recent study showed that the distributed LOC responses to objects remained stable across 60° rotations (Eger et al. 2008). Presently, there is no consensus across experimental findings in the degree to which ventral stream representations are view-dependent or view-invariant. These variable results may reflect differences in the neural representations depending on object category and cortical region, and/or methodological differences across studies (e.g., level of object rotation and fMRI-A paradigm used).

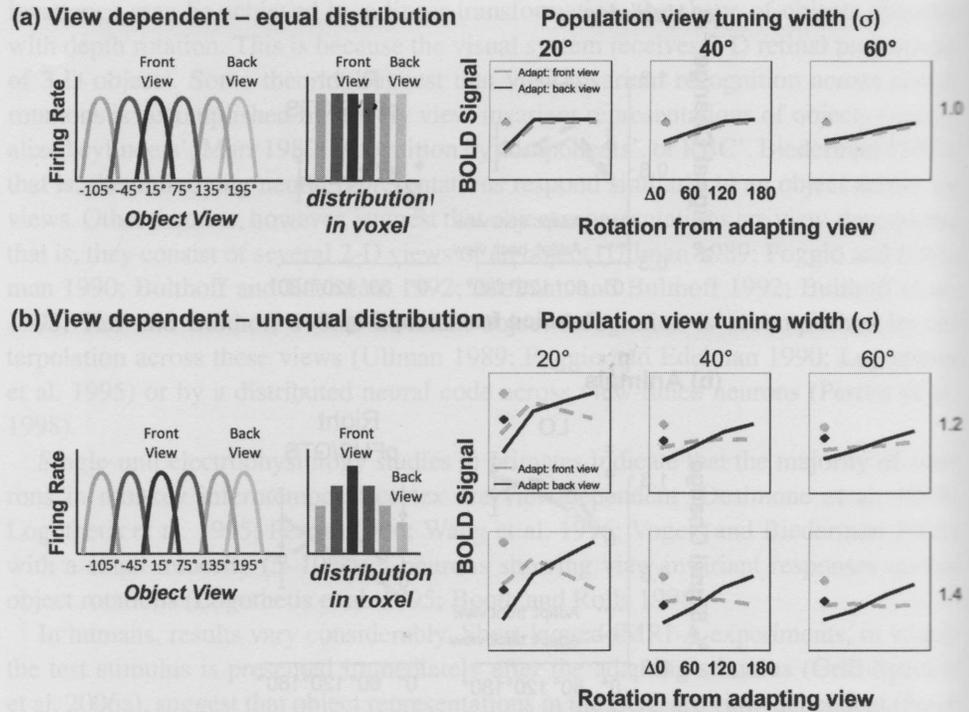
We addressed these differential findings in a recent study in which we used a parametric approach to investigate sensitivity to object rotation and a computational model to link putative neural tuning and resultant fMRI signals (Andresen et al. 2008, 2009). The parametric approach allows a richer characterization of rotation sensitivity because, rather than characterizing representations as invariant or not invariant, it measures the degree of sensitivity to rotations. Using fMRI-A we measured viewpoint sensitivity as a function of the rotation level for two object categories – animals and vehicles. Overall, we found sensitivity to object rotation in the LOC, but there were differences across categories and regions. First, there was higher sensitivity to vehicle rotation than to animal rotation. Rotations of 60° produced a complete recovery from adaptation for vehicles, but rotations of 120° were necessary to produce recovery from adaptation for animals (Fig. 6.6). Second, we found evidence for overrepresentation of the front view of animals in the right pFus/OTS: its responses to animals were



**Figure 6.6.** LO responses during fMRI-A experiments of rotation sensitivity. Each line represents response after adapting with a front (dashed black) or back view (solid gray) of an object. The nonadapted response is indicated by the diamonds (black for front view, and gray for back view). The open circles indicate significant adaptation, lower than nonadapted,  $P < 0.05$ , paired  $t$ -test across subjects. (a) Vehicle data. (b) Animal data. Responses are plotted relative to a blank fixation baseline. Error bars indicate SEM across eight subjects. Adapted from Andreson, Vinberg, and Grill-Spector (2009).

higher for the front view than the back view (compare black and gray circles in Fig. 6.6(b) right). In addition fMRI-A effects across rotation varied according to the adapting view (Fig. 6(b) right). When adapting with the back view of animals, we found recovery from adaptation for rotations of 120° or larger, but when adapting with the front view of animals, there was no significant recovery from adaptation across rotations. One interpretation is that there is less sensitivity to rotation when adapting with front views than back views of animals. However, the behavioral performance of subjects in a discrimination task across object rotations showed that they are equally sensitive to rotations (performance decreases with rotation level) whether rotations are relative to the front or back of an animal (Andresen et al. 2008), which suggests that this interpretation is unlikely. Alternatively, the apparent adaptation across a 180° rotation relative to a front animal view, may just reflect lower responses to a back animal view.

To better characterize the underlying representations and examine which representations may lead to our observed results, we simulated putative neural responses and predicted the resultant fMRI responses in a voxel. In the model, each voxel contains a mixture of neural populations, each of which is tuned to a different object view



**Figure 6.7.** Simulations predicting fMRI responses of putative voxels containing a mixture of view-dependent neural populations. *Left*, Schematic illustration of the view tuning and distribution of neural populations tuned to different views in a voxel. For illustration purposes we show a putative voxel with 4 neural populations. *Right*, Result of model simulations illustrating the predicted fMRI-A data. In all panels, the model includes 6 Gaussians tuned to specific views around the viewing circle, separated 60° apart. Across columns, the view tuning width varies. Across rows, the distribution of neural populations preferring specific views varies. *Diamond*, Responses without adaptation (black for back view, and gray for front view). *Lines*, Response after adaptation with a front view (dashed gray line) or back view (solid black line). (a) Mixture of view-dependent neural populations that are equally distributed in a voxel. Narrower tuning (left) shows recovery from fMRI-A for smaller rotations than wider view tuning (right). This model predicts the same pattern of recovery from adaptation when adapting with the front or back view. (b) Mixture of view-dependent neural populations in a voxel with a higher proportion of neurons that prefer the front view. The number on the right indicates the ratio between the percentages neurons tuned to the front versus the back view. Top row, ratio = 1.2. Bottom row, ratio = 1.4. Because there are more neurons tuned to the front view in this model, it predicts higher BOLD responses to frontal views without adaptation (gray vs. black diamonds) and a flatter profile of fMRI-A across rotations when adapting with the front view. Adapted from Andresen, Vinberg, and Grill-Spector (in press).

(Fig. 6.7 and Andresen et al. 2008, in press). fMRI responses were modeled to be proportional to the sum of responses across all neural populations in a voxel. We simulated the fMRI responses in fMRI-A experiments for a set of putative voxels that varied in the view-tuning width of neural populations, the preferred view of different neural populations, the number of different neural populations, and the distribution of populations tuned to different views within a voxel. Results of the simulations indicate that two main parameters affected the pattern of fMRI data: (1) the view-tuning width of the neural population, and (2) the proportion of neurons in a voxel that prefer a specific object view.

Figure 6.7(a) shows the response characteristics of a model of a putative voxel that contains a mixture of view-dependent neural populations that are tuned to different object views, in which the distribution of neurons tuned to different views is uniform. In this model, narrower tuning (left) shows recovery from fMRI-A for smaller rotations than wider view tuning (right). Responses to front and back views are identical when there is no adaptation (Fig. 6.7(a), diamonds), and the pattern of adaptation as a function of rotation is similar when adapting with the front or back views (Fig. 6.7(a)). Such a model provides an account of responses to vehicles across object-selective cortex (as measured with fMRI) and for animals in LO. Thus, this model suggests that the difference between the representation of animals and vehicles in LO is likely due to a smaller population view tuning for vehicles than for animals (a tuning width of  $\sigma < 40^\circ$  produces complete recovery from adaptation for rotations larger than  $60^\circ$ , as observed for vehicles). Figure 6.7(b) shows the effects of neural distributions on fMRI signals. Simulations predict that when there are more neurons in a voxel that are tuned to the front view, there will be higher BOLD responses to frontal views without adaptation (gray vs. black diamonds) and a flatter profile of fMRI-A across rotations when adapting with the front view, as observed in pFus/OTS for animals.

### 6.6.1 Implications for Theories of Object Recognition

Overall, our results provide empirical evidence for view-dependent object representation across human object-selective cortex that is evident with standard fMRI as well as fMRI-A measurements. These data provide important empirical constraints for theories of object recognition and highlight the importance of parametric manipulations for capturing neural selectivity to any type of stimulus transformation.

Given the evidence for neural sensitivity to object view, how is view-invariant object recognition accomplished? One appealing model for view-invariant object recognition is that objects are represented by a population code in which single neurons may be selective to a particular view, but the distributed representation across the entire neural population is robust to changes in object view (Perrett et al. 1998).

Does the view-specific approach necessitate a downstream view-invariant neuron? One possibility is that perceptual decisions may be performed by neurons outside visual cortex and these neurons are indeed view-invariant. Examples of such view-invariant neurons have been found in the hippocampus, perirhinal cortex, and prefrontal cortex (Freedman et al. 2001, 2003; Quiroga et al. 2005; Quiroga et al. 2008). Alternatively, operations based on the population code (or a distributed code) across view-tuned neurons may be sufficient for view-invariant decisions based on view-sensitive neural representations.

## 6.7 Debates About the Nature of Functional Organization in the Human Ventral Stream

So far we have considered general computational principles that are required by any object recognition system. Nevertheless, it is possible that some object classes or domains require specialized computations. The rest of this chapter examines functional

specialization in the ventral stream that may be linked to these putative "domain-specific" computations.

As illustrated in Figure 6.1, several regions in the ventral stream exhibit higher responses to particular object categories, such as places, faces, and body parts, compared to other object categories. The discovery of category-selective regions initiated a fierce debate about the principles of functional organization in the ventral stream. Are there regions in the cortex that are specialized for any object category? Is there something special about computations relevant to specific categories that generates specialized cortical regions for these computations? In other words, perhaps some general processing is applied to all objects, but some computations may be specific to certain domains and may require additional brain resources. We may also ask about how these category-selective regions come about: Are they innate, or do they require experience to develop?

Four prominent views have emerged to explaining the pattern of functional selectivity in the ventral stream. The main debate centers on the question of whether regions that elicit maximal response for a category are a module for the representation of that category, or whether they are part of a more general object recognition system.

### 6.7.1 Limited Category-Specific Modules and a General Area for All Other Objects

Kanwisher and coworkers (Kanwisher 2000; Op de Beeck et al. 2008) suggested that ventral temporal cortex contains a limited number of modules specialized for the recognition of special object categories such as faces (in the FFA), places (in the PPA), and body parts (in the EBA and FBA). The remaining object-selective cortex (LOC), which shows little selectivity for particular object categories, is a general-purpose mechanism for perceiving any kind of visually presented object or shape. The underlying hypothesis is that there are few domain-specific modules that perform computations that are specific to these classes of stimuli beyond what would be required from a general object recognition system. For example, faces, like other objects, need to be recognized across variations in their appearance (a domain-general process). However, given the importance of face processing for social interactions, there are aspects of face processing that are unique. Specialized face processing may include identifying faces at the individual level (e.g., John vs. Harry), extracting gender information, evaluating gaze and expression, and so on. These unique, face-related computations may be implemented in face-selective regions.

### 6.7.2 Process Maps

Tarr and Gauthier (2000) proposed 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 performed in localized cortical regions. For example, faces are usually recognized at the individual level (e.g., "That is Bob Jacobs"), but many objects are typically recognized at the category level (e.g., "That is a horse"). Following this reasoning, and evidence that objects of expertise activate the FFA more than other objects

(Gauthier et al. 1999; Gauthier et al. 2000), Gauthier, Tarr, and their colleagues 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 (Gauthier et al. 1999; Gauthier et al. 2000; Tarr and Gauthier 2000).

### 6.7.3 Distributed Object-Form Topography

Haxby and colleagues (2001) posited an "object-form topography," in which the occipitotemporal cortex contains a topographically organized representation of shape 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 and colleagues 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 ventrottemporal cortex. Further, they showed that it is possible to predict what object category the subjects viewed, even when regions that show maximal activation to a particular category (e.g., the FFA) were excluded (Haxby et al. 2001). Thus, this model suggests that the ventrottemporal cortex represents object category information in an overlapping and distributed fashion.

One of the reasons that this view is appealing is that a distributed code is a combinatorial code that allows representation of a large number of object categories. Given Biederman's rough estimate that humans can recognize about 30,000 categories (Biederman 1987), this provides a neural substrate that has a capacity to represent such a large number of categories. Second, this model posited a provocative view that when considering information in the ventral stream, one needs to consider the weak signals as much as the strong signals, because both convey useful information.

### 6.7.4 Topographic Representation

Malach and colleagues (2002) suggested that eccentricity biases underlie the organization of ventral and dorsal stream object-selective regions because they found a correlation between category preference (higher response to one category over others) and eccentricity bias (higher response to a specific eccentricity than to other eccentricities (Levy et al. 2001; Hasson et al. 2002; Hasson et al. 2003). Regions that prefer houses to other objects also respond more strongly to peripheral stimulation than to foveal stimulation. In contrast, regions that prefer faces or letters respond more strongly to foveal stimulation than to peripheral stimulation. Malach and colleagues (Malach et al. 2002) proposed that the correlation between category selectivity and eccentricity bias is driven by spatial-resolution needs. Thus, objects whose recognition depends on analysis of fine details are associated with foveal representations, and objects whose recognition requires large-scale integration are associated with peripheral representations. To date, however, there is no clear evidence that eccentricity biases in the FFA are also coupled with better representation of high spatial frequency or smaller receptive fields or, conversely, that the PPA prefers low spatial frequencies or contains neurons with larger receptive fields.

Presently, there is no consensus in the field about which account best explains the functional organization of the ventral stream. Much of the debate centers on the degree

to which object processing is constrained to discrete modules or involves distributed computations across large stretches of the ventral stream (Op de Beeck et al. 2008). The debate is about the spatial scale on which computations for object recognition occur as well as the fundamental principles that underlie specialization in the ventral stream.

On the one hand, domain-specific theories need to address findings of multiple foci that show selectivity. For example, multiple foci in the ventral stream respond more strongly to faces than to objects; thus, a strong modular account of a single “face module” for face recognition is unlikely. Also, the spatial extent of these putative modules is undetermined, and it is unclear whether each of these category-selective regions corresponds to a visual area. Further, high-resolution fMRI (1–2 mm on a side) shows that the spatial extent of category-selective regions is smaller than that estimated with standard fMRI (3–4 mm on a side) and that these regions appear more patchy (Schwarzlose et al. 2005; Grill-Spector et al. 2006b).

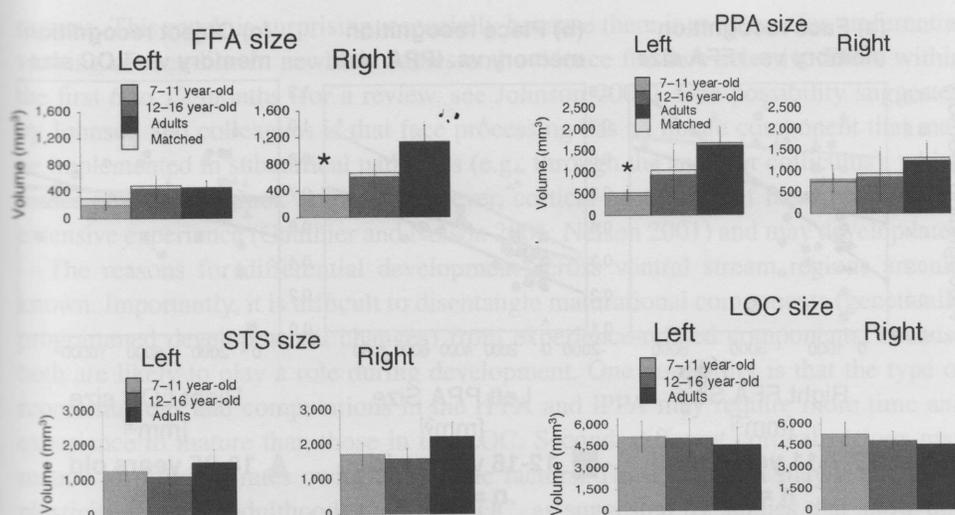
On the other hand, a potential problem with very distributed and overlapping account of object representation in the ventral stream is that, in order to resolve category information, the brain may need to read out information present across the entire ventral stream (which is inefficient). Further, the fact that there is information in the distributed response does not mean that the brain uses the information in the same way that an independent classifier does. It is possible that activation in localized regions is more informative for perceptual decisions than the information available across the entire ventral stream (Grill-Spector et al. 2004; Williams et al. 2007). For example, FFA responses predict when subjects recognize faces and birds but do not predict when subjects recognize houses, guitars, or flowers (Grill-Spector et al. 2004).

## 6.8 Differential Development of Category Selectivity from Childhood to Adulthood

One research direction that can shed light on these debates is an examination of the development of ventral stream functional organization. What is the role of experience in shaping category selectivity in the ventral stream?

### 6.8.1 fMRI Measurements of the Development of the Ventral Stream

To address these questions, our lab (Golarai et al. 2007) identified face-, place-, and object-selective regions within individual children (7–11 years old), adolescents (12–14 years old), and adult subjects (18–35 years old) while subjects fixated and reported infrequent events when two consecutive images were identical (one-back task). We found a prolonged development of the right FFA (rFFA) and left PPA (lPPA) that manifested as an expansion of the spatial extent of these regions across development from age 7 to adulthood (Fig. 6.8). The rFFA and lPPA were significantly larger in adults than in children, with an intermediate size of these regions in adolescents. Notably, the rFFA of children was about a third of the adult size, but it was still evident in 85% of children. These developmental changes could not be explained by smaller anatomical cortical volumes of the fusiform gyrus or the parahippocampal

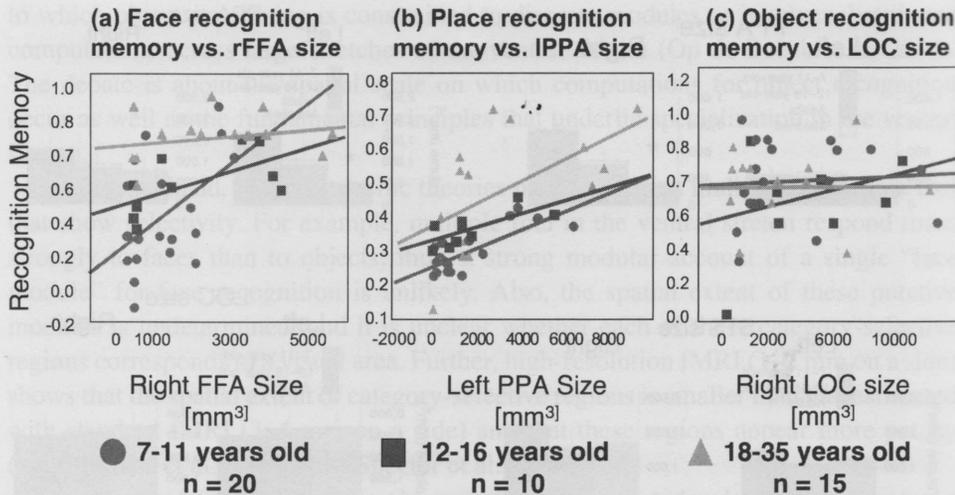


**Figure 6.8.** Volume of the rFFA, IPPA, STS, and LOC across children, adolescents, and adults. Filled bars indicate average volume across all subjects, which include 20 children, 10 adolescents, and 15 adults. Open bars indicate the average volumes for the subset of subjects that were matched for BOLD-related confounds and include 10 children, 9 adolescents, and 13 adults. Error bars indicate SEM across subjects. Asterisks indicate significantly different than adult,  $P < 0.05$ . Note that different panels have different scales on the y-axis. Adapted from Golarai et al. 2007.

gyrus (Golarai et al. 2007), which were similar across children and adults, or higher BOLD-related confounds in children (i.e., larger fMRI-related noise or larger subject motion; see Golarai et al. 2007; Grill-Spector et al. 2008) because results remained the same for a subset of subjects that were matched for fMRI-related confounds across ages. These developmental changes were specific to the rFFA and IPPA, because we found no differences across ages in the size of the LOC or the size of the pSTS face-selective region. Finally, within the functionally defined FFA, PPA, and LOC, there were no differences across ages in the level of response amplitudes to faces, objects, and places.

We also measured recognition memory outside the scanner and found that that face- and place-recognition memory increased from childhood to adulthood (Golarai et al. 2007). Further, face-recognition memory was significantly correlated with rFFA size (but not the size of other regions) in children and adolescents (but not adults), and place-recognition memory was significantly correlated with IPPA size (but not the size of other regions) in each of the age groups (Fig. 6.9). These data suggest that improvements in face- and place-recognition memory during childhood and adolescence are correlated with increases in the size of the rFFA and IPPA, respectively.

Another recent study (Scherf et al. 2007) examined the development of the ventral stream in children (5–8 years old), adolescents (11–14 years old), and adults using movie clips that contained faces, objects, buildings, and navigation. Using group analysis methods, they reported the absence of face-selective activations (vs. objects, buildings, and navigation) in 5- to 8-year-old children in both the fusiform gyrus and the pSTS. The lack of FFA in young children in the group analysis may be due to the smaller and more variable FFA location in children, which would affect its detection



**Figure 6.9.** Recognition memory versus size of rFFA, iPPA, and LOC. (a) Recognition memory for faces was significantly better in adults than children ( $*P < 0.0001$ ) or adolescents ( $**P < 0.03$ ). Adolescents' memory for faces was better than children's ( $**P < 0.03$ ). Recognition memory for places was better in adults than in children ( $†P < 0.0001$ ). Adolescents' memory for places was better than children's ( $†P < 0.01$ ). Recognition accuracy for objects was not different across age groups. Error bars indicate SEM. (b) Recognition memory for faces versus FFA size. Correlations are significant within children and adolescents ( $r > 0.49$ ,  $P < 0.03$ ), but not adults. (c) Recognition memory of places versus PPA size. Correlations are significant within each age group ( $r > 0.59$ ,  $P < 0.03$ ). (d) Recognition memory for objects versus LOC size. No correlations were significant ( $P > 0.4$ ). Adapted from Golarai et al. 2007.

in a group analysis. Indeed when Scherf and colleagues performed individual subject analysis, they found face-selective activations in 80% of their child subjects, but the extent of activations was smaller and more variable in location compared to those in adults. Like Golarai and colleagues, they found no difference in the spatial extent or level of response amplitudes to objects in the LOC. Unlike Golarai and colleagues, they reported no developmental changes in the PPA. The variant results may be due to differences in stimuli (pictures vs. movies), task (one-back task vs. passive viewing), and analysis methods (single subject vs. group analysis) across the two studies. For example, Golarai and colleagues instructed subjects to fixate and perform a one-back task. In this task, children had the same accuracy as adults but were overall slower in their responses, with no differences across categories. In the Scherf study, subjects watched movies, and performance was not measured during the scan. It is possible that the children had differential different eye movements or levels of attention than the adults, and this affected their findings.

### 6.8.2 Implications of Differential Development of Visual Cortex

Overall, fMRI findings suggest differential developmental trajectories across the human ventral visual stream. Surprisingly, these data suggest that more than a decade is necessary for the development of an adult-like rFFA and iPPA. This suggests that experience over a prolonged time may be necessary for the normal development of these

regions. This viewing of the first 6 to by Johnson a be implement biases newbo extensive exp The reason known. Impo programmed both are like representatio experience t mature at di plasticity (ev FFA respons 2000). Four differ among

In sum, neu object repre organization regions in o the neural n Many qu sitivity to o Do biases i pirical evid lead to bet second qu is experien stream? Th temporal s what comp object reco a particula expanse? high spati what is th the connec et al. 199 visual ar ing a mo

regions. This result is surprising, especially because there is evidence for preferential viewing of face-like in newborn babies and evidence for face-selective ERPs within the first 6 to 12 months (for a review, see Johnson 2001). One possibility suggested by Johnson and colleagues is that face processing has an innate component that may be implemented in subcortical pathways (e.g., through the superior colliculus), which biases newborns to look at faces. However, cortical processing of faces may require extensive experience (Gauthier and Nelson 2001; Nelson 2001) and may develop later.

The reasons for differential development across ventral stream regions are unknown. Importantly, it is difficult to disentangle maturational components (genetically programmed developmental changes) from experience-related components, because both are likely to play a role during development. One possibility is that the type of representations and computations in the rFFA and IPPA may require more time and experience to mature than those in the LOC. Second, different cortical regions may mature at different rates owing to genetic factors. Third, the FFA may retain more plasticity (even in adulthood) than the LOC, as suggested by studies that show that FFA responses are modulated by expertise (Gauthier et al. 1999; Tarr and Gauthier 2000). Fourth, the neural mechanisms underlying experience-dependent changes may differ among LOC, FFA, and PPA.

## 6.9 Conclusion

In sum, neuroimaging research in the past decade has advanced our understanding of object representations in the human brain. These studies have identified the functional organization of the human ventral stream, shown the involvement of ventral stream regions in object recognition, and laid fundamental stepping stones in understanding the neural mechanisms that underlie invariant object recognition.

Many questions remain, however. First, what is the relationship between neural sensitivity to object transformations and behavioral sensitivity to object transformations? Do biases in neural representations produce biases in performance? For example, empirical evidence shows overrepresentation of the lower visual field in LO. Does this lead to better recognition in the lower visual field than in the upper visual field? A second question is related to the development of the ventral stream: To what extent is experience (vs. genes) necessary for shaping functional selectivity in the ventral stream? Third, do object representations remain plastic in adulthood? If so, what is the temporal scale of plasticity, and are experience-induced changes long-lasting? Fourth, what computations are implemented in the distinct cortical regions that are involved in object recognition? Does the "aha" moment in recognition involve a specific response in a particular brain region, or does it involve a distributed response across a large cortical expanse? Combining experimental methods such as fMRI and MEG will provide both high spatial and temporal resolution, which is critical to addressing this question. Fifth, what is the pattern of connectivity between ventral stream visual regions? Although the connectivity in monkey visual cortex has been explored extensively (Van Essen et al. 1990; Moeller et al. 2008), we know little about the connectivity between cortical visual areas in the human ventral stream. This knowledge is necessary for building a model of hierarchical processing in humans and any neural network model of

object recognition. Approaches that combine methodologies, such as psychophysics with fMRI, MEG with fMRI, or DTI with fMRI, will be instrumental in addressing these fundamental questions.

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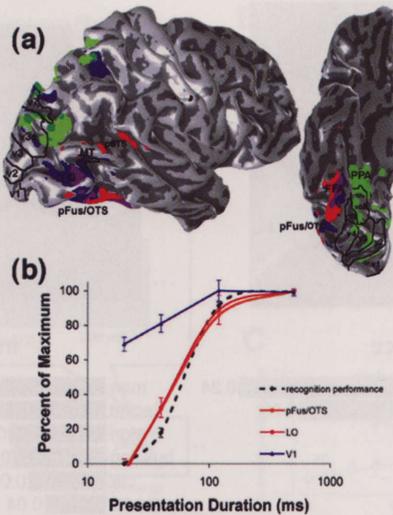
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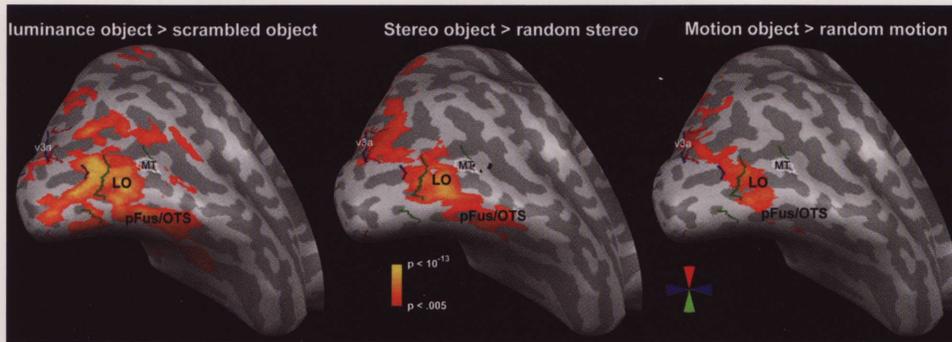
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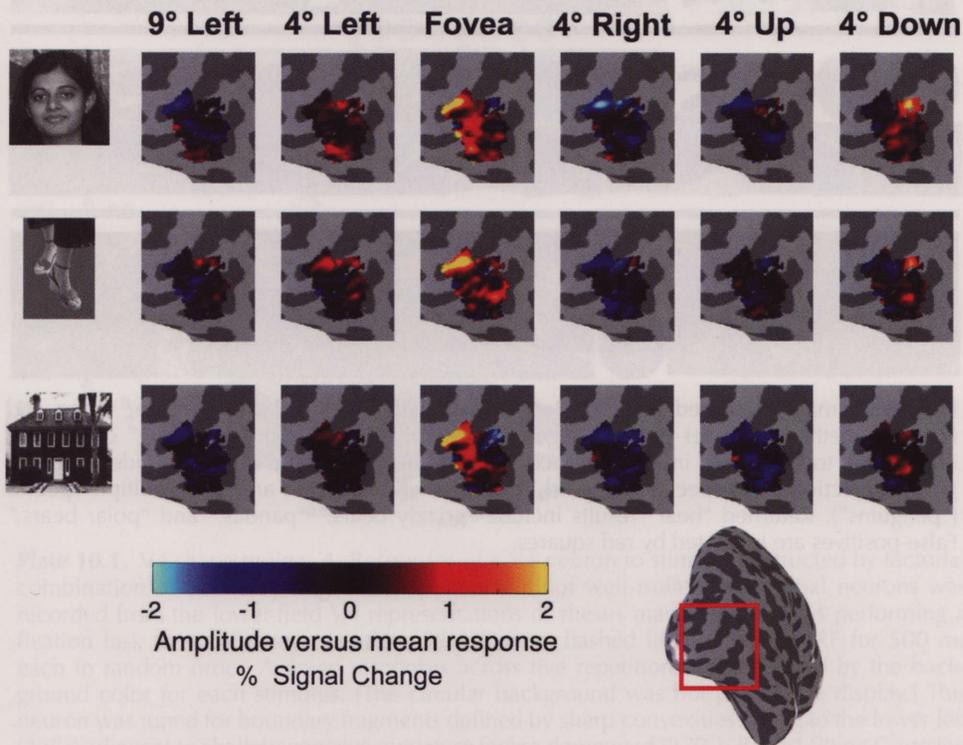


**Plate 6.1.** Object-, face-, and place-selective cortex. (a) Data of one representative subject shown on her partially inflated right hemisphere: lateral view (*left*); ventral view (*right*). *Dark gray* indicates sulci. *Light gray* indicates gyri. *Black lines* delineate retinotopic regions. *Blue regions* delineate object-selective regions (objects > scrambled objects), including LO and pFus/OTS ventrally as well as dorsal foci along the intraparietal sulcus (IPS). *Red regions* delineate face-selective regions (faces > non-faces objects), including the FFA, a region in LOS and a region in posterior STS. *Magenta regions* delineate overlap between face- and object-selective regions. *Green regions* delineate place-selective regions (places > objects), including the PPA and a dorsal region lateral to the IPS. *Dark green regions* delineate overlap between place- and object-selective regions. All maps thresholded at  $P < 0.001$ , voxel level. (b) LO and pFus/OTS (but not V1) responses are correlated with recognition performance (Grill-Spector et al. 2000). To superimpose recognition performance and fMRI signals on the same plot, all values were normalized relative to the maximum response for the 500-ms duration stimulus.

For fMRI signals (blue, red, and orange lines) =  $\frac{\% \text{signal}(\text{condition})}{\% \text{signal}(500 \text{ ms})}$ . For recognition performance (black) =  $\frac{\% \text{correct}(\text{condition})}{\% \text{correct}(500 \text{ ms})}$ .



**Plate 6.2.** Selective responses to objects across multiple visual cues across the LOC. Statistical maps of selective response to object from luminance, stereo and motion information in a representative subject. All maps were thresholded at  $P < 0.005$ , voxel level, and are shown on the inflated right hemisphere of a representative subject. (a) Luminance objects > scrambled objects. (b) Objects generated from random dot stereograms versus structureless random dot stereograms (perceived as a cloud of dots). (c) Objects generated from dot motion versus the same dots moving randomly. Visual meridians are represented by *red* (upper), *blue* (horizontal), and *green* (lower) lines. *White contour* indicates a motion-selective region, or MT. Adapted from Vinberg and Grill-Spector 2008.



**Plate 6.4.** LO distributed response patterns to different object categories and stimulus positions. Data are shown on the lateral aspect of the right hemisphere cortical surface for a representative subject. Each panel shows the distributed LO fMRI amplitudes after subtracting from each voxel its mean response. *Red and yellow*, Responses that are higher than the voxel's mean response. *Blue and cyan*, Responses that are lower than the voxel's mean response. *Inset*, Inflated right cortical hemisphere, with red square indicating the zoomed region. Note that pattern changes significantly across columns (positions) and to a lesser extent across rows (categories). Adapted from Sayres and Grill-Spector 2008.