

The Ventral Visual Object Pathway in Humans: Evidence from fMRI

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WE HUMANS CAN RECOGNIZE an object within a fraction of a second, even if we have never seen that exact object before and even if we have no advance clues about what kind of object it might be (Potter, 1976; Thorpe et al., 1996). The cognitive and neural mechanisms underlying this remarkable ability are not well understood, and current computer vision algorithms still lag far behind human performance. One promising strategy for attempting to understand human visual recognition is to characterize the neural system that accomplishes it: the ventral visual pathway, which extends from the occipital lobe into inferior and lateral regions of the temporal lobe. Here I describe research from neuroimaging on humans that has begun to elucidate the general organization and functional properties of the cortical regions involved in visually perceiving people, places, and things.

I will focus on two main questions in this review. First, what is the functional organization of the ventral visual pathway? This pathway has been characterized in some detail in the macaque using single-unit recording. However, very little was known about its organization in humans even a few years ago, when functional magnetic resonance imaging (fMRI) studies of this region began. Other chapters in this volume review the organization of this pathway in macaques, as well as the organization of earlier retinotopic regions in human visual cortex (see Chapters 32 and 34). This review will focus on the segment of the human ventral visual pathway that lies anterior to retinotopic cortex. I will argue that this pathway contains a small number of category-specific regions, each primarily involved in processing a specific stimulus class, in addition to a more general-purpose region that responds to any kind of visually presented object.

Second, what is the nature of the representations we extract from visually presented objects? This question is at the heart of any theory of object recognition and has long been addressed using behavioral methods such as priming. fMRI is beginning to provide some clues about the nature of the visual representations that are extracted in each region. The technique of fMRI adaptation (Grill-Spector et al., 2000; Naccache and Dehaene, 2001) enables us to determine the invariances and equivalence classes of neural representations of objects within each region of cortex scanned.

Other techniques are beginning to address the question of whether objects are represented in distributed neural codes that span much of the ventral visual pathway or whether some kinds of objects are represented in focal regions of cortex.

Functional organization: category-selective regions

This section describes work that has characterized three distinct regions in the human ventral visual pathway, each of which responds selectively to a single category of visual stimuli (Fig. 79.1).

FACES Faces are enormously rich and biologically relevant stimuli, providing information not only about the identity of a person but also about his or her mood, age, sex, and direction of gaze. Indeed, behavioral studies of normal subjects and neurological patients (see Farah, 2000, for a review), as well as event-related potentials in humans (Allison et al., 1999; Bentin et al., 1996) and single-unit recording in monkeys (Perrett et al., 1982; Chapter 78, this volume), provide evidence that face perception engages cognitive and neural mechanisms distinct from those engaged during the recognition of other classes of objects. Several brain imaging studies (e.g., Haxby et al., 1991; Puce et al., 1995, 1996; Sergent et al., 1992) described cortical regions that were most active during viewing of faces. However, these studies did not include the kinds of control conditions that are necessary for testing whether the activated regions are selectively involved in face perception.

Kanwisher et al. (1997) scanned subjects with fMRI while they viewed rapidly presented sequences of faces versus sequences of familiar inanimate objects. We found a region in the fusiform gyrus in most subjects, and a second region in the superior temporal sulcus in about half of the subjects, that produced a stronger MR response during face viewing than object viewing (see also McCarthy et al., 1997). A greater response to faces than to objects could be produced by processes that have nothing to do with face perception per se, including attentional engagement, which may be greater for faces than for nonfaces, a general response to anything animate or anything human, or a response to the

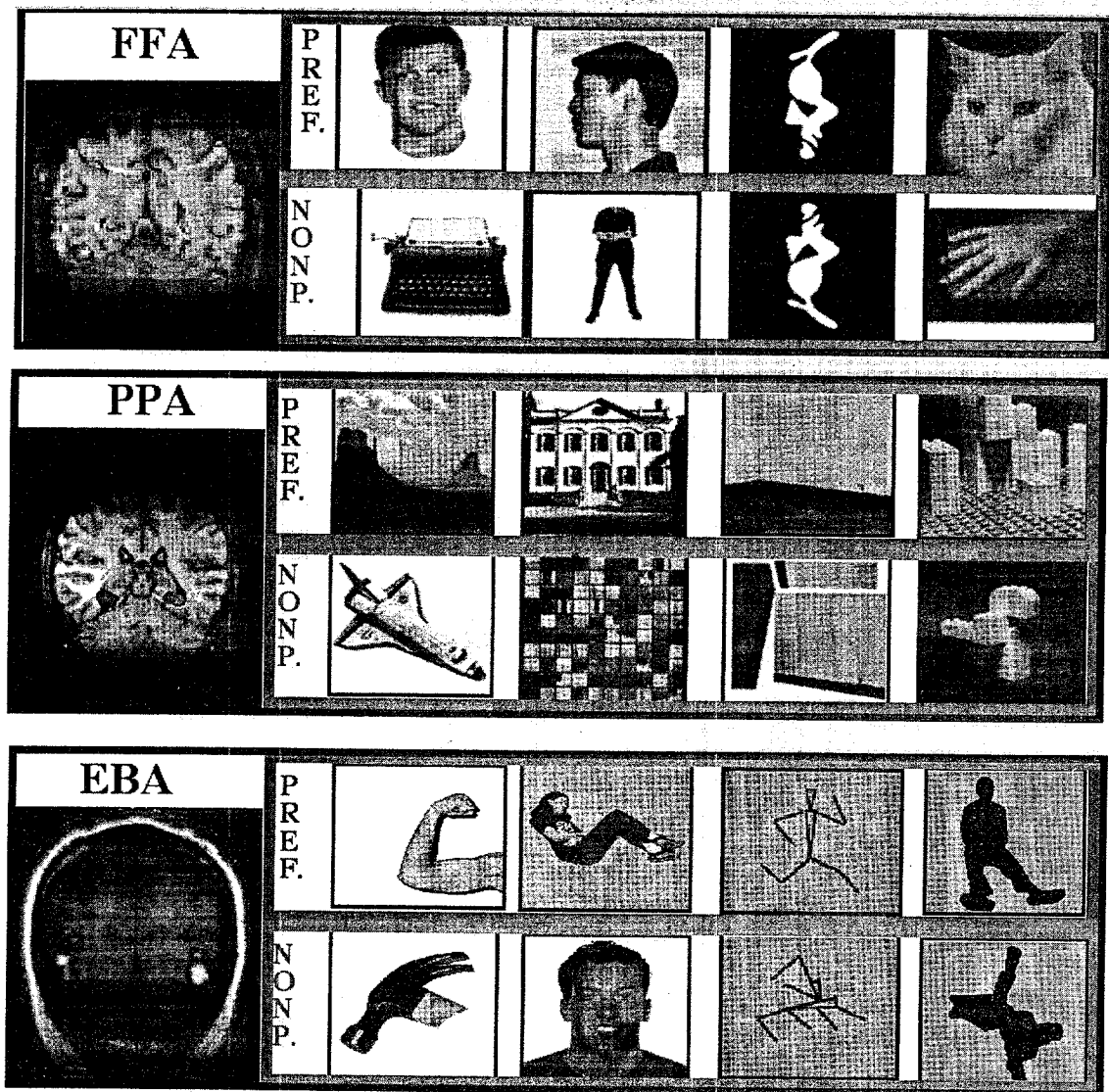


FIGURE 79.1. Three category-selective regions in human extrastriate cortex. The brain images at the left show coronal slices in individual subjects; overlaid in color are regions that responded significantly more strongly to faces than to objects (the FFA), to scenes than to objects (the PPA), and to body parts than to object parts (the EBA). Each region responds to a wide variety of exemplars of

the category; for each area, four examples of such preferred stimuli are shown in the blue box at the top. Examples of nonpreferred stimuli for each area (that elicit about half the response of preferred stimuli in terms of percent age signal increase from a fixation baseline) are indicated in the red box at the bottom. (See color plate 55.)

low-level visual features present in face stimuli. To test these and other hypotheses, we first identified the candidate face-selective fusiform region individually in each subject with the comparison of faces to objects, and then measured the response in this region of interest (ROI) to a number of subsequent contrasting conditions. After demonstrating that the same region responded at least twice as strongly to faces as to any of the other control stimuli, we concluded that this region is indeed selectively involved in face processing and named it the *fusiform face area* (FFA) (Fig. 79.1, top, and Fig. 79.2, bottom). The claim that the FFA responds selectively or specifically to faces does not mean that it responds *exclu-*

sively to faces. Although the FFA responds much more to faces than to objects, it responds more to objects than to a baseline condition such as a fixation point. The standard criterion for neural selectivity (Tovee et al., 1993), adopted here, is that the response must be at least twice as great for the preferred stimulus category as for any other stimulus category.

By now, the FFA has been studied extensively in many different experiments and labs. These studies generally agree that the FFA responds more strongly to a wide variety of face stimuli (e.g., front-view photographs of faces, line drawings of faces, cat faces, cartoon faces, and upside-down faces)

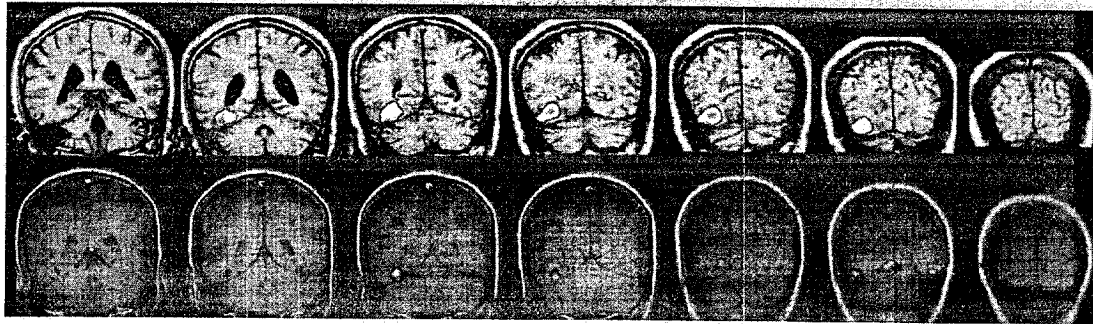


FIGURE 79.2. The top row (adapted from Figure 1 of Wada and Yamamoto, 2001) shows the site of a lesion (outlined in red for greater visibility) that produced a severe deficit in face recognition but not in object recognition. The bottom row shows the author's FFA (color indicates regions responding significantly more strongly during face viewing than object viewing). Note the similarity in the anatomical locus of the lesion and the FFA activation, suggesting that an intact FFA may be necessary for face but not object recognition. (See color plate 56.)

than to various nonface control stimuli, even when each of these (like faces) constitutes multiple similar exemplars of the same category, including houses (Haxby et al., 1999; Kanwisher et al., 1997), hands (Kanwisher et al., 1997), animals, provided that their heads are not visible (Kanwisher et al., 1999; but see Chao et al., 1999), flowers (McCarthy et al., 1997), or cars (Halgren et al., 1999). These effects are similar when the subject is merely passively viewing the stimuli or carrying out a demanding discrimination task on them (Kanwisher et al., 1997), suggesting that the response does not arise from a greater attentional engagement by faces than by other stimuli. Nor can the FFA response to faces be accounted for in terms of a low-level feature confound, as the response is higher when a face is perceived versus not perceived even when the stimulus is unchanged, as in binocular rivalry (Tong et al., 1998) and face-vase reversals (Hasson et al., 2001).

While the basic response properties of the FFA are generally agreed upon, the function of this region is not. The most basic question is whether the function of the FFA is truly specific to faces or whether it involves a domain-general operation that could in principle be applied to other stimuli (despite being more commonly carried out on faces). For example, in our original paper on the FFA, we suggested testing whether it could be activated by inducing holistic encoding on nonface stimuli. Rossion et al. (2000) found that although attending to whole faces, rather than parts of faces, enhanced the right (but not left) FFA response, attending to whole houses, rather than parts of houses, did not. These data argue against the domain-general holistic encoding hypothesis, instead implicating the right FFA in processing holistic/configural aspects of faces.

Gauthier and her colleagues have argued for a somewhat different domain-general hypothesis, according to which the right FFA is specialized for discriminating between any structurally similar exemplars of a given category for which the subject is an expert (Tarr and Gauthier, 2000). However, most of her evidence is based on studies using novel stimuli

called *Greebles*, a suboptimal choice for testing this hypothesis because they have the same basic configuration as a face (i.e., a symmetrical configuration in which two horizontally arranged parts are above two vertically aligned central parts, as in the configuration of eyes, nose, and mouth). Nonetheless, in one study, Gauthier et al. (1999) found that the FFA was activated by cars in car fanatics and birds in bird experts; this result was replicated by Xu et al. (Xu and Kanwisher, 2001). However, in both studies the effect sizes are small, and the response to faces remains about twice as high as the response to cars in car experts, a result that is consistent with both the face-specificity hypothesis and the subordinate-level-categorization-of-structurally-identical-exemplars-for-which-the-subject-is-expert¹ hypothesis. Stronger evidence on this debate comes from a double dissociation in neurological patients: face recognition impairments can be found in the absence of impairments in the expert discrimination of category exemplars (Henke et al., 1998) and vice versa (Moscovitch et al., 1997). These findings argue that different cortical mechanisms are involved in face perception and in the expert visual discrimination of structurally similar category exemplars (Kanwisher, 2000).

If the face specificity of the FFA is granted, the next question is what exactly the FFA does with faces. The FFA appears not to be involved specifically in discriminating the direction of eye gaze, because it is more active during attention to face identity than to gaze direction, while the face-selective region in the superior temporal sulcus responds more strongly in the opposite comparison (Hoffman and Haxby, 2000). Nor is the FFA likely to be specifically involved

¹Note that if any of these descriptors is removed, the hypothesis has already been disproved: the low FFA response to words shows that visual expertise is not sufficient, and the low FFA response during hand or house discrimination shows that subordinate-level discrimination of structurally identical exemplars is not sufficient to explain the high response to faces.

in extracting emotional expressions from faces, given the consistently high response of the FFA during viewing of expressionless faces. In studies directly manipulating the presence or absence of emotional expressions in face stimuli, the greatest activation is in the amygdala (Breiter et al., 1996) or anterior insula (Phillips et al., 1997), not the fusiform gyrus. Another hypothesis is that the FFA represents semantic rather than perceptual information (Martin and Chao, 2001). However, this too seems unlikely because (1) this region does not respond more to a familiar face, for which semantic information about the individual is available, than to an unfamiliar face, for which it is not (Gorno-Tempini and Price, 2001; Shah et al., 2001), and (2) this region does not appear to represent abstract semantic information about people in general, as it responds no more when subjects read paragraphs describing people than when they read paragraphs describing inanimate objects, though this same comparison produces robust activation in the superior temporal sulcus (R. Saxe and N. Kanwisher, unpublished data). Thus, the FFA appears not to be involved specifically in extracting information about gaze direction or emotional expression, or to be involved in representing semantic information about individual people.

Evidence that this area may be involved in simply detecting the presence of a face comes from the findings that activity in the FFA is strong even for inverted faces (Aguirre et al., 1999; Haxby et al., 1999; Kanwisher et al., 1998) and for line drawings of faces (A. Harris and N. Kanwisher, unpublished data; see also Halgren et al., 1999; Ishai et al., 1999), both of which support easy face detection but not face recognition. However, another study (K. Grill-Spector and N. Kanwisher, unpublished data) found that activity in the right FFA is correlated with both successful detection and successful categorization of faces (versus nonfaces) and in successful discrimination between individual faces, suggesting that it is involved in both of these abilities.

PLACES For navigating social primates like humans, one other visual ability is arguably as important as recognizing faces: determining our location in the environment. A region of cortex called the *parahippocampal place area* (PPA) appears to play an important role in this ability (Epstein and Kanwisher, 1998). The PPA responds strongly whenever subjects view images of places, including indoor and outdoor scenes, as well as more abstract spatial environments such as urban "scenes" made out of Legos, virtual spaces depicted in video games (Aguirre et al., 1996; Maguire et al., 1998), or close-up photographs of desktop scenes (P. Downing, R. Epstein, and N. Kanwisher, unpublished data). Remarkably, the visual complexity and number of objects in the scenes are unimportant; the response is just as high to bare empty rooms (two walls, a floor, and sometimes a door or window) as it is to complex photos of the same rooms completely fur-

nished. The PPA also responds fairly strongly to images of houses cut out from their background (though less than to full scenes), presumably because spatial surroundings are implicit in a depiction of a house. Thus, it is information about the spatial layout of the scene that is apparently critical to the PPA response (Fig. 79.1, *middle*).

Patients with damage to parahippocampal cortex often suffer from *topographical disorientation*, an impairment in wayfinding (Aguirre and D'Esposito, 1999; Epstein et al., 2001; Habib and Sirigu, 1987). The core deficit in these patients is an inability to use the appearance of places and buildings for purposes of orientation, perhaps implicating the PPA in place recognition. However, we tested a neurological patient with no PPA and largely preserved place perception but an apparent deficit in learning new place information, suggesting that the PPA may be more critical for encoding scenes into memory than for perceiving them in the first place (Epstein et al., 2001). This possibility is consistent with evidence from other laboratories suggesting that parahippocampal cortex is involved in memory encoding of words (Wagner et al., 1998) and scenes (Brewer et al., 1998).

The PPA is apparently not engaged in processes that rely on knowledge of the specific environment (such as planning a route to a particular location in one's stored cognitive map of the world), as it responds with the same strength to familiar versus unfamiliar places: Epstein et al. (1999) presented MIT students and Tufts University students with scenes from the MIT and Tufts campuses, and found no difference in the response to the same images when they depicted familiar rather than unfamiliar places. Interestingly, however, a significantly higher response was found in the PPA to familiar than to unfamiliar buildings cut out from their background, perhaps because the spatial background was more likely to be inferred in a familiar scene.

One attractive idea is that the PPA may constitute the neural instantiation of a previously hypothesized system for spatial reorientation (Cheng, 1986; Hermer and Spelke, 1994). When disoriented rats and human infants must search for a hidden object, they rely largely on the shape of the local environment to reorient themselves and find the object (but see Gouteux et al., 2001; Learmonth et al., 2001). Strikingly, they completely ignore informative landmark cues such as the location of a salient visual object or feature. This led Cheng and others to hypothesize the existence of a *geometric module* that represents the shape (but not other features) of surrounding space for the purpose of reorientation. The exclusive use of spatial layout information, and not object/landmark information, is tantalizingly reminiscent of the much greater activation of the PPA by images of spatial layouts than images of objects.

How is the PPA related to the two other neural structures most commonly implicated in spatial encoding and navigation, the hippocampus and the parietal lobe? It has been

hypothesized that the hippocampus contains a cognitive map of the animal's environment (O'Keefe and Nadel, 1978). In contrast, the parietal lobe has been implicated in representing the specific spatial information that is relevant to guiding current action. In keeping with this division of labor, physiological recordings in animals indicate that the hippocampus contains allocentric (world-centered) representations of place, whereas the parietal lobes contain egocentric (body-centered) representations of spatial locations (Burgess et al., 1999). For example, *place cells* in the rat hippocampus respond when the animal is in a specific location in its environment, largely independent of which way the animal is facing, while *spatial view cells* in the primate hippocampus respond when the animal views a given spatial location (Georges-François et al., 1999). In contrast, neurons in the primate parietal cortex apparently represent space in a number of egocentric coordinates tied to the location of the retina, hand, or mouth (Colby and Goldberg, 1999). A recent study found that fMRI adaptation to repeated stimuli in the PPA occurs only when the same view of a scene is repeated, implicating the PPA in egocentric rather than allocentric representations of space (Epstein et al., 2003).

In sum, although it is now well established that the PPA responds selectively to information about spatial layouts and places, it remains unclear what exactly the PPA does with this information. Critical questions for future research concern the role of the PPA in reorientation and encoding of spatial information into memory, as well as the nature of the interactions between the PPA, the hippocampus, and the parietal lobe.

BODIES Our latest addition to the set of category-selective regions of cortex is the extrastriate body area (EBA) (Downing et al., 2001). This region responds about twice as strongly when subjects view images depicting human bodies or body parts (nothing too interesting!) as when they view objects or object parts (Fig. 79.1, *bottom*). The EBA is found in all subjects in the right (and sometimes also the left) lateral occipitotemporal cortex on the lower lip of the posterior superior temporal sulcus, just superior to area MT/MST. The EBA's response profile is unlikely to reflect low-level stimulus confounds, as the same region responded about twice as strongly to body as to nonbody stimuli even when the two stimulus sets were visually similar (e.g., stick figures versus rearranged versions of stick figures that no longer corresponded to body configurations; silhouettes of people versus slightly rearranged silhouettes). Further experiments showed that the EBA does not simply respond to anything living, animate, or known to be capable of motion, or to any object with parts that can move relative to each other: the EBA responds more to human bodies than to trees, mammals, or objects with movable parts such as scissors, staplers, and corkscrews. The one exception to the body

specificity of the EBA is the fact that this region responds no more to faces than to objects. As expected from this result, the EBA does not overlap much, if at all, with the face-selective region in the superior temporal sulcus.

At present, the function of the EBA is unknown. It may be involved in recognizing individuals (when their faces are hidden or far away), or in perceiving the body configuration of other people, or even in perceiving the location of one's own body parts. The EBA is suggestively close to area MT, perhaps implicating it in integrating information about body shape and motion (Grossman et al., 2000). The EBA is also close to other regions that have been shown to be activated during social perception, from discriminating the direction of eye gaze, to perceiving or inferring intentions, to perceiving human voices. Thus the EBA may be part of a broader network of nearby areas involved in social perception and social cognition.

WHAT ELSE? How many category-selective regions of cortex exist in the human visual pathway? Other categories including animals and tools have been reported to selectively activate focal regions of cortex (Martin and Chao, 2001). However, the evidence is not as strongly established in these cases. When only a few stimuli have been compared, apparent category selectivity must be treated cautiously. For example, we found a region that responded more strongly to chairs than to faces or places, replicating the findings of Ishai et al. (1999), but the same region responded just as strongly to pictures of food, animals, and flowers. In ongoing work in our lab, we have tested well over a dozen categories (P. Downing and N. Kanwisher, unpublished data); so far, we have found no other regions of cortex that exhibit the strong category selectivity typical of the FFA, PPA, and EBA. Thus, it appears that faces, places, and bodies may be unusual in the way they are processed and represented in the cortex. The apparent lack of other category-selective regions of cortex raises the question of how other kinds of objects are represented.

Functional organization: category-general regions

Considerable evidence suggests that in addition to the category-specific regions described previously, human visual cortex contains a region more generally involved in perceiving the shape of any kind of object. A large region of lateral and inferior occipital cortex just anterior to retinotopic cortex [the lateral occipital complex (LOC)] responds more strongly to stimuli depicting shapes than to stimuli with similar low-level features that do not depict shapes (Kanwisher et al., 1996; Malach et al., 1995; see Grill-Spector et al., 2001, for a review). Importantly, the response in this region was the same for familiar and unfamiliar shapes, so the response cannot be straightforwardly

accounted for in terms of matching to stored visual representations, or semantic or verbal coding of the stimuli. Common areas within this lateral occipital region are activated by shapes defined by motion, texture, and luminance contours (Grill-Spector et al., 1998a; Grill-Spector et al., 1998b). Several studies have implicated the LOC in visual object recognition by showing that activity in this region is correlated with success on a variety of object recognition tasks (Bar et al., 2001; Grill-Spector et al., 2000; James et al., 2000; Lerner et al., 2002). Thus, an investigation of the response properties of the LOC may provide important clues about the nature of the representations underlying object recognition.

Several studies have shown a reduction in the response of a particular region of the LOC (and other regions of cortex) when stimuli are repeated. Grill-Spector et al. (1999) further showed that in the LOC this effect (*fMRI adaptation*) can be observed even when the repeated shapes vary in size and position, demonstrating that the representations in this area are largely invariant with respect to changes in size and position. While this adaptation effect was not found across changes in object viewpoint or direction of illumination in this study, another recent study by Vuilleumier et al. (2002) found that the left fusiform gyrus (but not the right) exhibited invariance to viewpoint. Kourtzi and Kanwisher (2001) further demonstrated adaptation in this region between stimulus pairs that had different contours but the same perceived shape (because of changes in occlusion), but not between pairs with identical contours that differed in perceived shape (because of a figure-ground reversal). These findings suggest that neural populations in the LOC represent the perceived shape of an object in a fashion invariant to changes in position and size but not viewpoint (at least in the right hemisphere). Given the correlation of the MR signal in this region with successful recognition, representations with these properties are likely to play an important role in human object recognition.

Other studies have shown that the response in this region declines as images of familiar objects are cut into pieces and the positions of those pieces are rearranged. However, interestingly, most regions within the LOC do not show much decline in the magnitude of the MR response until images are broken into at least 16 fragments (Lerner et al., 2001), suggesting that neural populations in these regions are fragment-based rather than holistic. At the same time, the response of the LOC is strongly affected by more global factors such as object completion, with higher responses to partly occluded line drawings that can be completed compared to those that cannot (Lerner et al., 2002). Another intriguing recent study found that a small region within the LOC responds to objects compared to textures in both visual and haptic modalities, although most of the LOC responds preferentially to only visually presented objects (Amedi et al., 2001).

Anatomically, the LOC is close to and sometimes partly overlapping with the FFA (on the ventral surface) and the EBA (on the lateral surface). Note that such overlap does not imply any contradiction in the data; it simply indicates that some voxels respond significantly more strongly to faces than to nonface objects (and hence are included in the FFA) or to bodies than to objects (and hence are included in the EBA), while the same voxels also respond significantly more strongly to nonface objects than to scrambled objects (and hence are included in the LOC). However, such overlap does indicate that functional definitions of this sort do not serve to categorize uniquely each region of cortex. One account of this situation is that the FFA, EBA, and the LOC are in fact part of the same functional region, which is composed of a set of category-selective and/or feature-selective columns (Fujita et al., 1992) at such a fine scale that they cannot be resolved with fMRI, except for a few very large such regions such as the FFA. Another possibility is that the FFA and LOC (and the EBA and LOC) do not in fact overlap anatomically, with the apparent overlap due to limitations in the spatial resolution of fMRI.

In sum, it appears that the ventral visual pathway contains one region, the LOC, that responds strongly to object structure but that exhibits little selectivity for specific object categories, along with a small number of category-specific modules (for faces, places, bodies, and perhaps a few others yet to be discovered). Indeed, it would seem a sensible design for the cortex to supplement its general-purpose mechanisms for describing the shape of any kind of visually presented object (i.e., the LOC) with a small number of additional more specialized mechanisms, each of which may be designed to handle the unique computational challenges posed by stimuli of a specific kind.

Important open questions

As the previous sections suggest, neuroimaging in humans has taught us much about the functional organization of the ventral visual pathway and about the representations involved in object recognition. However, some of the most important and difficult questions remain to be tackled. Next, I outline some of these questions and the ongoing experimental work that is attempting to address them.

DISTRIBUTED VERSUS LOCAL REPRESENTATIONS OF OBJECTS
Many of the studies described in previous sections follow a common strategy in visual neuroscience of inferring the function of a cortical area, voxel, or neuron from the stimulus that drives it most strongly. However, this strategy is viable only to the extent that maximal responses carry most of the information in a neural representation.

Thus, an important unresolved question concerns the functional significance of the "nonpreferred" responses in

the cortical regions discussed above. For example, do the low but nonzero responses to nonfaces in the FFA reflect a critical involvement of the FFA in the detection or recognition of nonface objects? Haxby et al. (1999) have argued that the partial response to nonfaces is "problematic for [Kanwisher et al.'s] hypothesis that face-selective regions . . . constitute a 'module specialized for face perception'" (p. 196). However, there are at least two reasons why it need not be problematic. First, because of limitations on the spatial resolution due to voxel size, blood flow regulation, and other factors, the MR signal intensity from a particular region should not be expected to reflect a pure measure of the activity in a single functional module, but will include contributions from functionally distinct adjacent (or interleaved) neural tissue. Second, there is no reason to expect even a strongly face-selective cortical area to shut itself off completely when a nonface is presented. Indeed, it is hard to imagine how this could occur without an additional gating mechanism that discriminates between faces and nonfaces and allows only face information into the region in question. In the absence of such a gating mechanism, it would be most natural to expect a low but positive response to nonfaces in a region of cortex specialized for face processing. Thus, the mere existence of nonpreferred responses does not argue against the functional specificity of the region they are recorded from. The critical questions we must answer to understand nonpreferred responses are (1) do they carry information? and (2) is this information used? A recent paper by Haxby et al. (2001) addresses the first question.

Haxby et al. (2001) used fMRI to scan subjects while they viewed eight different categories of stimuli. The data from each subject were then split in half, with the data from odd runs in one set and the data from even runs in the other set (the same stimuli were used in odd and even runs). In this fashion, two "partner" activation maps were generated for each of the eight stimulus categories (i.e., 16 activation maps per subject). Next, Haxby et al. carried out seven pairwise comparisons for each activation map, each testing whether that activation map was more similar to its partner (in the other data set) than to each of the activation maps from the other seven categories. In this fashion, the performance on activation map categorization was quantified as the percentage of these pairwise comparisons that were categorized "correctly," that is, in which the target map was more similar to its partner than to the other map. Haxby et al. found high accuracy in activation map categorization, demonstrating that the patterns of activation for each category were highly replicable within individual subjects. More importantly, they argued that when only the region that responded maximally to a given category was included in the analysis, categorization performance in determining which of the nonpreferred categories had been presented was still well above chance. They therefore suggested that "regions such as the 'PPA' and

'FFA' are not dedicated to representing only spatial arrangements or human faces, but, rather, are part of a more extended representation for all objects."

However, Haxby et al. did not carry out the analyses necessary to support this conclusion. Spiridon and Kanwisher (2002) replicated their main result, and also compared performance levels for discriminations involving faces and houses and discriminations between pairs of inanimate objects. We found that the FFA supports accurate discrimination between faces and nonfaces but performs at near-chance levels on discriminations between inanimate objects. Similarly, the PPA contains sufficient information for accurate discrimination of houses versus other objects but performs at near-chance levels on discriminations between nonpreferred stimuli. Further, on discriminations between small inanimate objects, neither the FFA nor the PPA outperforms retinotopic cortex, suggesting that any small amount of discriminative information concerning nonpreferred stimuli that may exist in these areas is likely to be based on low-level features that are confounded with stimulus category rather than on true abstract category information. Thus, although some object information may be distributed across the ventral visual pathway, we find no evidence that the FFA and PPA carry any real categorical information about nonpreferred stimuli.

Of course, these investigations are subject to two important limitations characteristic of all fMRI research. First, each voxel in the fMRI data contains hundreds of thousands of neurons, so it is possible that discriminative information for nonpreferred categories might exist in these regions at a finer spatial scale. Second, fMRI data (like neurophysiological recordings) are purely correlational, so even when information is present in a given cortical region, we cannot be sure that it forms a critical part of the representation.

A recent neuropsychological study addresses both problems for the case of the FFA. Wada and Yamamoto (2001) describe a neurological patient with an unusually circumscribed lesion restricted to the region of the right FFA (Fig. 79.2). This man was severely impaired on face recognition but had fully preserved object recognition. If we assume that his lesion included the right FFA, these data suggest that the FFA plays a necessary role in face but not object recognition (see also Barton et al., 2002). Thus, even if a small amount of category-discriminative information for nonfaces exists in the FFA of normal subjects (undetected in the Spiridon-Kanwisher study), this information appears not to play any necessary role in the recognition of those nonface objects.

WHAT DOES CORTICAL MODULARITY TELL US ABOUT VISUAL RECOGNITION? Even if we can determine that some categories of objects are primarily recognized within focal regions of cortex selectively responsive to those categories, will this tell us much about how visual recognition works?

Does the mere existence of a specialized cortical region for a given category imply that qualitatively distinct processing mechanisms are involved in recognizing stimuli from that category?

One might argue that special-purpose mechanisms for processing a particular stimulus class would be expected only if the recognition of stimuli from that class poses new computational problems that could not be handled by existing general-purpose mechanisms. Connectionist researchers have noted the computational efficiency gained by the decomposition of a complex function into natural parts (Jacobs, 1999), and cortical specializations for components of visual recognition are plausible candidates for such task decomposition. If visual cortex is organized in such a computationally principled fashion, then each of the modular components of the system we discover with functional imaging could be expected to instantiate a distinct set of computations.

However, an alternative hypothesis is that visual cortex contains a large number of stimulus-selective regions (such as the feature columns in inferotemporal cortex reported by Tanaka, 1997), but the computations that go on in each of these regions are very similar. On this view, cortical specialization might be found for virtually any stimulus class, yet these specializations might not imply qualitative differences in the processing of these stimulus classes. A critical goal for future research is to determine whether the functional organization of visual recognition is better characterized by this kind of *shallow specialization*, or whether it reflects a deeper form of functional decomposition in which each of a small number of functionally specific regions carries out a qualitatively distinct computation in the service of an evolutionarily or experientially fundamental visual process.

ORIGINS OF SPECIALIZED REGIONS WITHIN THE VENTRAL VISUAL PATHWAY Where do cortical specializations come from? Does functional differentiation within the ventral visual pathway arise from experience-dependent self-organization of cortex (Jacobs, 1997), or are these cortical specializations partly innately specified? For faces, places, and bodies, this question is hard to answer because both experiential and evolutionary arguments are plausible. Despite recent misattributions to me of innatist claims about the origins of the FFA (Pierce et al., 2001; Tarr and Gauthier, 2000), my view is that we have almost no relevant data on this question and are in no position to make any strong claims about the origins of the FFA.

On the one hand, experience must surely play some role in the development of face areas, given the ample evidence that neurons in the ventral visual pathway are tuned by experience. On the other hand, at least some aspects of face perception appear to be innately specified, as newborn infants preferentially track schematic faces compared to visually

similar scrambled faces (Johnson et al., 1991). However, these two observations leave open a vast space of possible ways that genes and environment could interact in the construction of a selective region of cortex such as the FFA.

What does seem pretty clear is that the development of normal adult face processing (and thus, by hypothesis, the development of the FFA) is heavily constrained both anatomically and chronologically. First, neuropsychological patients who selectively lose face recognition abilities as a result of focal brain damage are rarely if ever able to relearn this ability, suggesting that the remaining visual cortex (which is adequate for visual recognition of nonface objects) cannot be trained on face recognition in adulthood. Further, this inability to shift face mechanisms to alternative neural structures may be set very early in development, as evidenced by a patient who sustained damage to the fusiform region when only 1 day old, and who as an adult now has severe difficulties in the recognition of faces (and some other object categories) (Farah et al., 2000). Evidence that very early experience is also crucial in the development of normal adult face recognition comes from a remarkable recent study by Le Grand et al. (2001), who tested people born with dense bilateral cataracts. These people had no pattern vision until their cataracts were surgically corrected between 2 and 6 months of age. After surgery, pattern vision was excellent, if not quite normal. Surprisingly, these individuals never developed normal configural processing of faces. As adults, they are impaired at discriminating between faces that differ in the relative positions of facial features, despite being unimpaired at discriminating faces on the basis of individual face parts. (They are also unimpaired or on either task relative to normal controls when the face stimuli are presented upside down.) Thus, pattern vision in the first few months of life is necessary for the development of normal face processing as an adult; years of subsequent visual experience with faces are not sufficient.

One intriguing part of the puzzle comes from recent reports of *developmental prosopagnosic* patients, who have no brain damage discernible from MRI images or life histories but who are severely impaired at face recognition. These individuals generally do not have other cognitive impairments and often have few or no other impairments in other visual tasks (Duchaine, 2000; Nunn et al., 2001). Although many of these people report relatives with similar deficits, it is not known whether this syndrome is heritable. Thus, it is not yet clear whether it arises from subtle brain damage that cannot be detected on MRIs, or from alterations in genes that code specifically for the construction of a normal face recognition system, or from a failure of general developmental mechanisms that normally lead to the functional differentiation of neural tissue based on experience. Another clue comes from two recent studies showing that autistic subjects exhibit different patterns of cortical activation when

they view faces from those found in normal subjects (Pierce et al., 2001; Schultz et al., 2000). But as with developmental prosopagnosia, this finding can be explained in terms of either experience or genetic factors, or both.

One way to unconfound genetic and experiential factors in the development of category-specific regions of cortex is to consider a category for which a specific role of genes is unlikely: visual word recognition. People have been reading for only a few thousand years, which is probably not long enough for natural selection to have produced specialized machinery for visual word recognition. Thus, strong evidence for a region of cortex selectively involved in the visual recognition of letters or words would provide proof that experience alone with a given category of stimulus, without a specific genetic predisposition, can be sufficient for the construction of a region of cortex that is selectively involved in the recognition of stimuli of that category. Some evidence has been reported for cortical specializations for visually presented letters (Polk and Farah, 1998) and words (Cohen et al., 2000). However, preliminary work in our lab suggests otherwise: cortical regions that respond to visually presented words do not show the kind of selectivity seen in the FFA, PPA, and EBA (J. Jovicich and N. Kanwisher, unpublished data). Thus, for the case of visual recognition in humans, it is not yet clear whether it is the experience of the individual or the experience of the species (or both) that is critical for the construction of functionally distinct regions in the ventral visual pathway.

Conclusions

In just the past few years, functional neuroimaging has taught us a great deal about the organization of the ventral visual pathway in humans. Three new category-specific regions of cortex (the FFA, PPA, and EBA), as well as another category-general region (the LOC), have been discovered and described in some detail. But despite this rapid progress, fundamental questions remain unanswered. fMRI has taught us little or nothing about the perceptual functions each of these newly described regions is critical for, the connections between each of these areas and the rest of the brain, the developmental origins of these areas, or the actual mechanisms that occur in each and how they collectively accomplish object recognition.

On the other hand, new methods are being developed at a rapid rate and hold the promise of real progress in answering many of these questions. The integration of fMRI with event-related potential and magnetoencephalography data may provide the temporal resolution that will be critical for understanding how visual computations unfold over time. The ability to scan children and perhaps even infants should enable us to trace the appearance and function of each of these areas over development. Patient studies and transcranial

magnetic stimulation in normal subjects provide methods for testing the necessity of each region for different visual recognition tasks. Finally, in one of the developments I find most pleasing, the once one-way flow of information from primate visual neuroscience to visual cognitive neuroscience in humans has recently become bidirectional, with fMRI studies in macaques now motivated and informed by prior work on humans (Tsao et al., 2001; Vanduffel et al., 2001).

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