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The lateral occipital complex and its role in object recognition

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Abstract

Here we review recent findings that reveal the functional properties of extra-striate regions in the human visual cortex that are involved in the representation and perception of objects. We characterize both the invariant and non-invariant properties of these regions and we discuss the correlation between activation of these regions and recognition. Overall, these results indicate that the lateral occipital complex plays an important role in human object recognition. © 2001 Published by Elsevier Science Ltd.

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1. Introduction

One of the greatest mysteries in cognitive science is the human ability to recognize visually-presented objects with high accuracy and lightening speed. Interest in how human object recognition works is heightened by the fact that efforts to duplicate this ability in machines have not met with extraordinary success. What secrets does the brain hold that underline its virtuosity in object recognition? Here, we review recent findings from functional brain imaging research that provide important clues from a region of the brain that appears to play a central role in human object recognition, the lateral occipital complex.

A natural way to make progress in understanding any complex system is to first try to discover its functional components. Brain imaging is well suited for this enterprise and has led to spectacular successes in mapping the brain regions involved in early and mid-level stages of visual information processing (Engel, Glover, & Wandell, 1997; Wandell, 1999; Heeger, 1999; Tootell, Hadjikhani, Mendola, & Marrett, 1998a). This strategy has also been applied to higher-level visual functions (for reviews, see Wojciulik & Kanwisher, 2000; Culham & Kanwisher, 2001) including object recognition (for

reviews, see Mazer & Gallant, 2000; Kanwisher, Downing, Epstein, & Kourtzi, 2001).

Several positron emission tomography (PET) studies conducted in the early 1990s have revealed selective activation of ventral and temporal regions associated with the recognition of faces and objects (Haxby, Grady, Horwitz et al., 1991; Sergent, Ohta, & MacDonald, 1992; Allison et al., 1994; Kosslyn et al., 1994; Allison, McCarthy, Nobre, Puce, & Belger, 1994) and attention to shapes (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Haxby et al., 1994). However, the exact location of these activation foci in relation to known retinotopic areas and the nature of the underlying representations contributing to object recognition remained unclear from these studies.

Malach et al. (1995) reported a cortical region that responds more strongly when subjects passively view photographs of common everyday objects than when they view visual textures without obvious shape interpretations. This region, which is located on the lateral bank of the fusiform gyrus extending ventrally and dorsally, was named the lateral occipital complex (LOC). Importantly, the magnitude of the response in this region was no different for familiar objects (e.g. a bear or a flower) and unfamiliar objects with clear three-dimensional shape interpretations (e.g. Henry Moore sculptures). A similar result was found by Kanwisher et al. (1996) using line drawings: stronger responses to 3D objects depicted in line drawings,

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whether familiar or novel, compared to scrambled line drawings, in which no clear shape interpretation was possible. The locus of the activation in the Kanwisher et al. study was more ventral and anterior to that of the Malach et al. study. However, several more recent studies (Grill-Spector et al., 1998; Grill-Spector, Kushnir, Edelman, Itzhak & Malach, 1998; Murtha, Chertkow, Beauregard & Evans, 1999; Kourtzi & Kanwisher, 2000a; Doniger, Foxe, Murray, Higgins, Snodgrass & Schroeder, 2000) provide evidence that the entire region, beginning in lateral occipital cortex and extending anteriorly and ventrally into posterior temporal regions (see Fig. 1 and Fig. 6), responds more strongly to intact objects with clear shape interpretations than to control stimuli that do not depict clear shapes.

A series of elegant studies (Allison et al., 1994a; McCarthy, Puce, Belger, & Allison, 1999; Puce, Allison, & McCarthy, 1999; Allison, Puce, Spencer, & McCarthy, 1999) investigated related questions using event-related potentials recorded from electrodes placed directly on the cortical surface of patients prior to surgery. These studies found object-specific waveforms that show

stronger activation for a variety of objects (cars, flowers, hands and butterflies) than to scrambled control stimuli. They also reported in these studies of localized regions in the middle and anterior fusiform gyrus that exhibit face-specific responses as well as other sites that demonstrate letter-specific activations.

While the LOC is activated strongly when subjects view pictures of objects, this does not by itself prove that it is the locus in the brain that performs object recognition. Demonstrating that a specific cortical region responds to visual objects is necessary, but not sufficient for determining that it is a site of object recognition. Activation during object viewing could be due to other processes, such as visual attention, arousal, figure-ground segmentation, surface extraction, etc. However, evidence from lesion studies demonstrates that damage to the fusiform and occipito-temporal junction results in a variety of recognition deficits (Farah, Hammond, Mehta, & Ratcliff, 1989; Damasio, 1990; Damasio, Tranel, & Damasio, 1990; Farah, McMullen, & Meyer, 1991; Goodale, Milner, Jakobson, & Carey, 1991; Farah, 1992; Feinberg, Schindler, Ochoa, Kwan, &

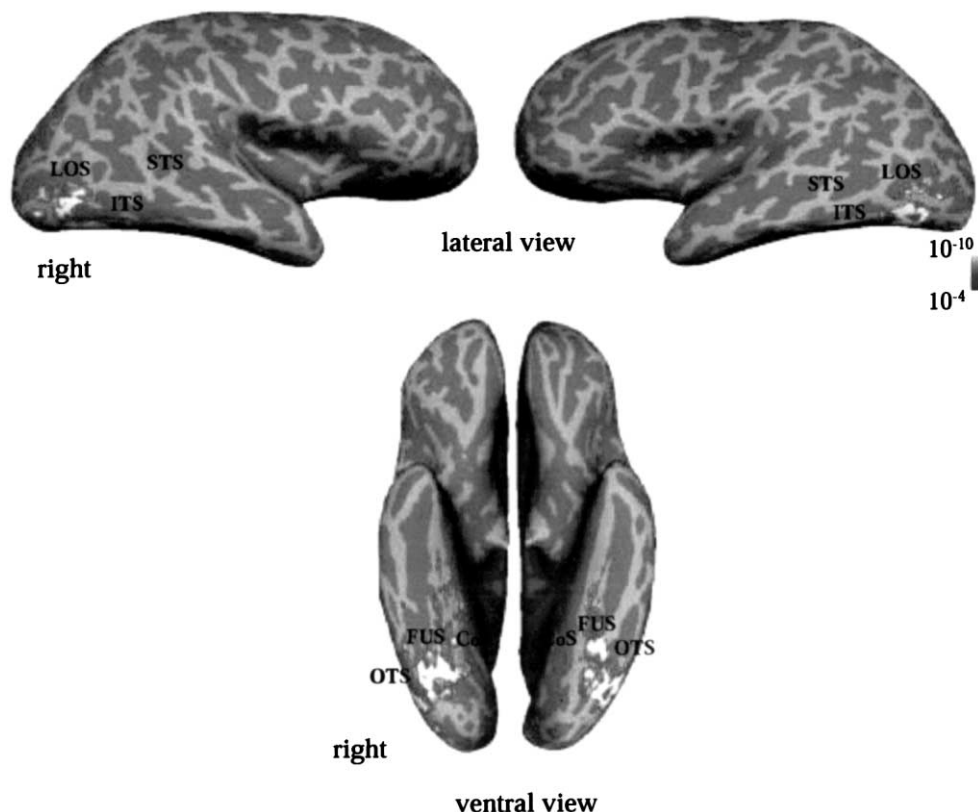


Fig. 1. Functional anatomy of the lateral occipital complex (LOC). Object selective regions depicted on the inflated brain of subject NT. The brain inflation algorithm was created by the Freesurfer and Ffast software packages developed at MGH, Charlestown, MA. The top panel illustrates the lateral view of the brain and the bottom panel the ventral view. These regions were defined by a t -test ($P < 10^{-4}$) that detected regions that were significantly more activated when subjects viewed photographs of cars or abstract sculptures compared to textures created by randomly scrambling these pictures into 400 blocks. Note that the object-selective activation appears bilaterally, on the lateral surface (LO) near the lateral occipital sulcus and in ventral occipito-temporal regions (LOa/pFs) extending into the posterior and mid fusiform gyrus and occipito-temporal sulcus. Abbreviations: LOS, lateral occipital sulcus; STS, superior temporal sulcus; ITS, inferior temporal sulcus; OTS, occipito-temporal sulcus; Fus, fusiform gyrus; COS, collateral sulcus.

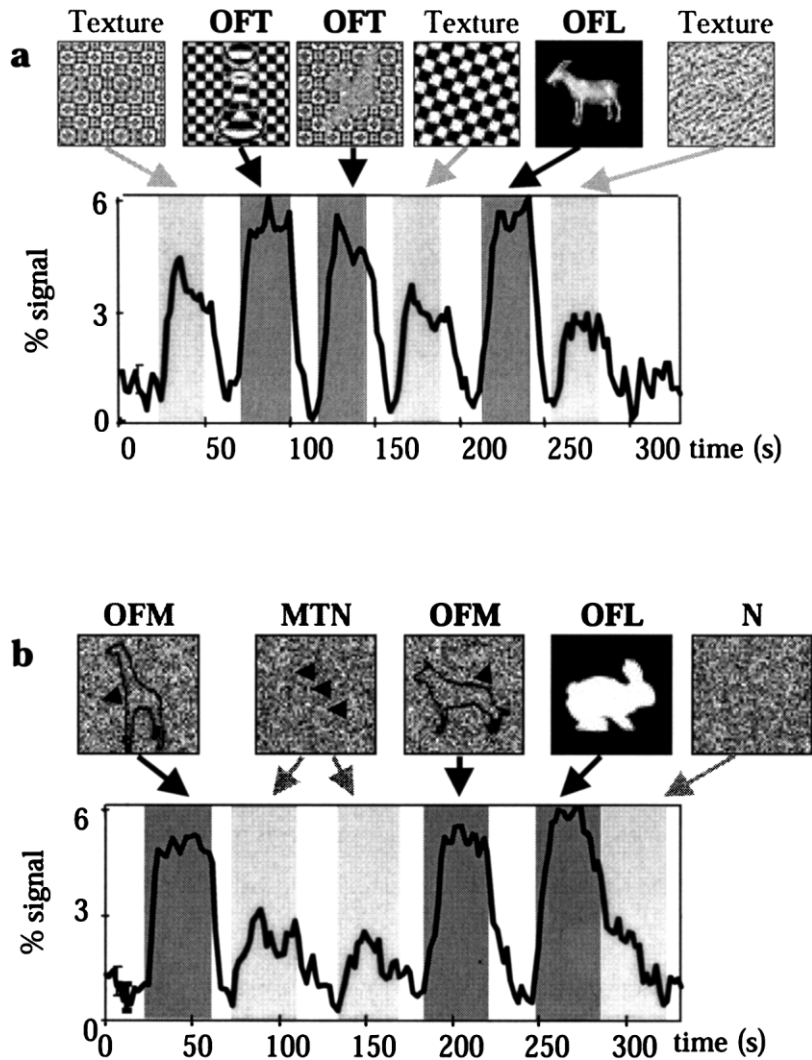


Fig. 2. Cue invariance in the LOC. Each of the two panels depicts the averaged timecourse across nine subjects extracted from object-selective foci defined functionally as areas activated preferentially by luminance defined objects compared to static textures or noise (N) ($P < 10^{-4}$). Nonetheless, these voxels also displayed stronger activation to both (a) objects defined by textures compared to textures and (b) objects defined from motion boundaries compared to coherently moving noise. Abbreviations: OFL, objects from luminance; OFT, objects from textures; OFM, objects from motion; MTN, coherently moving noise; N, static random noise patterns. Icons indicate the type of visual stimulation. In the OFM condition, the boundaries were created from motion and were not luminance boundaries as might seem from the image. For details see Grill-Spector et al. (1998a).

Farah, 1994; Farah, Klein, & Levinson, 1995; Moscovitch, Winocur, & Behrmann, 1999; Moscovitch et al., 1999). Also, studies in humans have shown that electric stimulation (Halgren, Wilson, & Stapleton, 1985; Puce et al., 1999) and repetitive transcranial stimulation (Stewart, Meyer, Frith, & Rothwell, 2001) of similar regions interferes with recognition processes or, in some cases, can create an illusory percept of an object or a face (Puce et al., 1999; Lee, Hong, Seo, Tae, & Hong, 2000). These findings suggest that these regions may be necessary (and perhaps even sufficient) for object recognition.

Object recognition is difficult and underconstrained because vision begins with 2D projections on the retina which could be cast by many possible 3D objects. Moreover, the appearance of the same object varies

considerably over changes in the viewing conditions, such as the illumination of the object or the viewing angle (Ullman, 1996). However, despite these changes we can recognize objects easily and rapidly (Thorpe, Fize, & Marlot, 1996; Grill-Spector, Kushnir, Hendler, & Malach, 2000). Thus, a robust recognition system, such as the human visual system, must be able to generalize across different instances of the same object. Yet, at the same time, it must be sensitive enough to discriminate between items that are similar and share common features, such as different car models or faces of different individuals. How is the representation of objects instantiated in the brain to allow both generalization across viewing conditions and fine discrimination between similar objects?

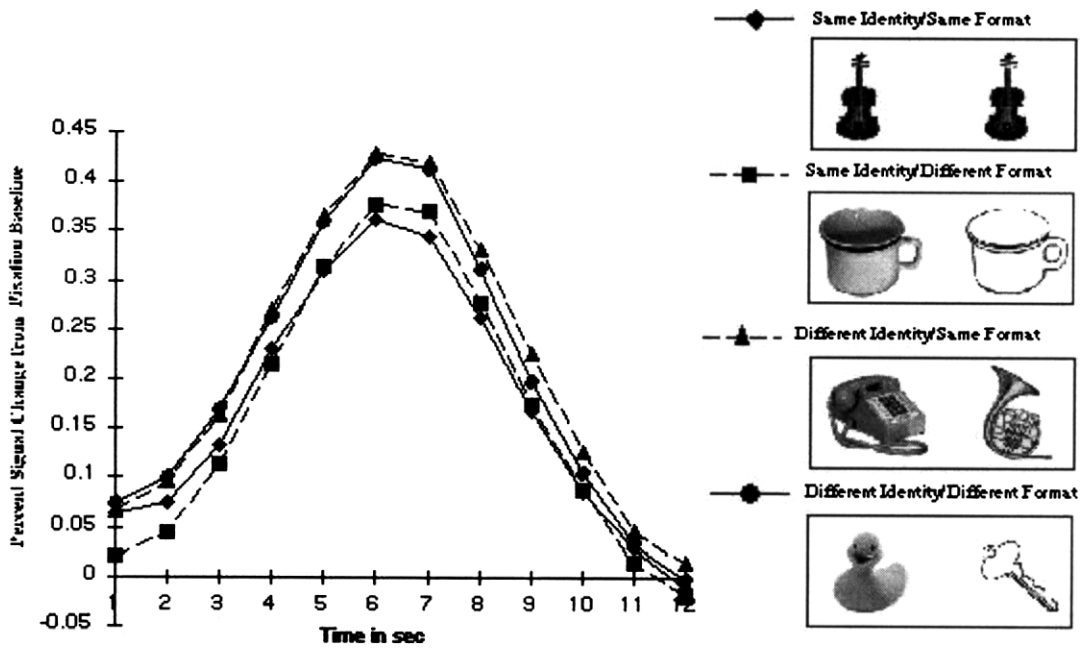


Fig. 3. Hemodynamic responses in LOC to pairs of same or different objects displayed either in the same or different format (gray scale or line drawings). Notice that when the same object is shown twice either in the same format or different formats, there is a reduced or adapted signal compared to trials in which different objects were shown either in the same or different formats.

We begin this review by describing the location and properties of regions in the human visual cortex that respond strongly when subjects view pictures of objects, but not to pictures of textures. Next, we review the cortical mechanisms that are involved in generalization across differences in the appearance of objects. In particular, we describe recent experiments using both conventional BOLD imaging, as well as a novel experimental paradigm known as fMR-adaptation (Grill-Spector & Malach, 2001) that characterize the invariant and non-invariant properties of the neural representation of objects in the LOC. Then, we discuss recognition processes that engage the LOC and the correlation between recognition and LOC activation. We end by discussing the current knowledge of the modular representation of certain object classes (faces and places) in the ventral stream.

2. Mapping object-selective visual areas in the human cortex

Is the LOC one visual area or many and what area/s is it homologous to in the macaque? Answering these questions is not straightforward and depends on one's definition of a visual area. In the macaque, visual areas are defined by multiple criteria, including function, retinotopy, anatomical connections and cytoarchitecture (for a review, see Felleman & Van Essen, 1991). However, less is known about the anatomical connectivity and physiology of the human brain than of the macaque (but see Clarke, Riahi-Arya, Tardif, Eskensky, & Probst, 1999).

For early visual cortex, retinotopy has provided a powerful guide, leading to plausible homologies between retinotopic visual areas in the human and the macaque. Early visual areas have a consistent topographic map of the external world that consists of either a quarter or half field representation in each hemisphere. Moreover, adjacent visual areas have a

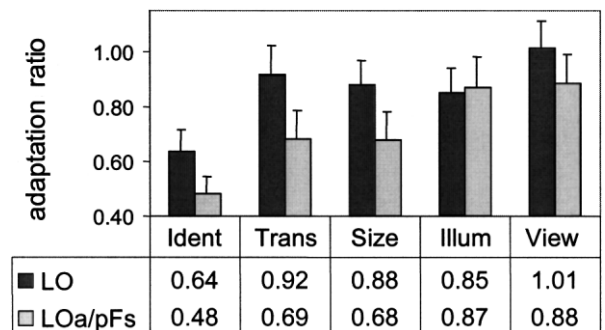


Fig. 4. Adaptation ratios for each condition calculated as the mean signal in an epoch of that condition divided by the mean signal in the different epoch consisting of different exemplars shown under the same viewing conditions. A ratio of 1.0 indicates no adaptation. Ratios that were significantly <1.0 indicate significant adaptation ($P < 0.01$) and are marked by asterisks. Error bars indicated 1 S.E.M. Note that both in LO and pFs/LOa there is adaptation due to repetitions of identical images. However, LO and LOa/pFs exhibit different levels of adaptation especially in the translation and size epochs (for details see Grill-Spector et al., 1999). Abbreviations: Ident: repetitions of identical pictures. Trans: the same object translated in the image plane. Size: the same object shown in different sizes. Illum: same object illuminated from five different directions. View: same object depicted from different viewing angles around the vertical axis.

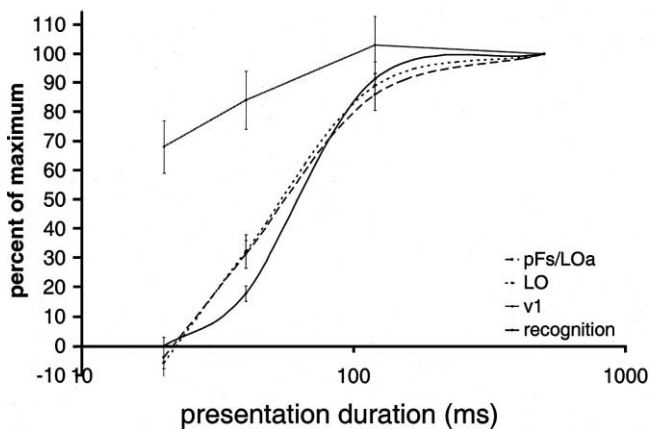


Fig. 5. The sensitivity of recognition and fMRI activation to object duration. In order to bring recognition and fMRI signal to a common scale we calculated the ratio of activation and recognition for each condition to the maximum observed (at 500 ms presentation). Solid black line: normalized recognition performance; x-axis: image duration on a logarithmic scale; graphs indicate average of 13 subjects, except for v1 that was calculated for six subjects; error bars indicate the S.E.M. Abbreviations: LO, lateral occipital; pFs, posterior fusiform; v1, primary visual cortex. For details see Grill-Spector et al. (2000).

mirror reversed representation of the visual world, which flips around the vertical and horizontal meridian at the boundaries between visual areas. These properties have been extensively used to produce replicable high-resolution retinotopic maps of individual subjects (Engel et al., 1994; DeYoe, Bandettini, Neitz, Miller, & Winans, 1994; Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997a). Beyond retinotopic cortex, functional criteria alone have been used to identify other visual areas in the human brain, such as the motion-selective area MT/MST (Watson et al., 1993; Tootell & Taylor, 1995), color-selective regions (labeled in different studies as either TEO/V4/V8) (Engel, Zhang, & Wandell, 1997b; Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998; Bartels & Zeki, 2000) and the kinetic motion area (area KO) (Van Oostende, Sunaert, Van Hecke, Marchal, & Orban, 1997). As we ascend up the visual pathway and are forced to rely on functional criteria, both the definitions of specific visual areas in the human brain and their homologies in the macaque become necessarily more speculative.

The LOC is a largely non-retinotopic area, activated by both the contralateral and ipsilateral visual fields (Grill-Spector et al., 1998b; Tootell, Mendola, Hadjikhani, Liu & Dale, 1998b). This area is located lateral and anterior to retinotopic regions and shows selectivity to both objects and object fragments (Grill-Spector et al., 1998b). These response properties are compatible with the receptive field profiles of inferotemporal (IT) neurons in the macaque, which respond to moderately complex to complex visual stimuli and have large receptive fields that partially overlap the fovea (Gross, Rocha, & Bender, 1972; Desimone, Albright, Gross, &

Bruce, 1984; Tanaka, 1993; Ito, Tamura, Fujita, & Tanaka, 1995).

Is the LOC a single functionally homogeneous area, or is it composed of several subdivisions? Recent results (Grill-Spector et al., 1999) indicate that the LOC might contain two spatially segregated subdivisions, a dorsal-caudal subdivision (LO) and a ventral-anterior subdivision located in the fusiform gyrus (pFs/LOa). LO (see Fig. 1, lateral view) is situated posterior to MT in the lateral-occipital sulcus and extends into the posterior inferior-temporal sulcus. This region is also located lateral to a lower field representation (Grill-Spector et al., 2000) and might exhibit some weak retinotopy, in that there are some regions within LO that are more responsive to the fovea and other regions that are more responsive to the periphery (Tootell, Hadjikhani, Mendola, Marett, & Dale, 1998). The anterior-ventral part of the LOC (termed LOa or pFs, see Fig. 1, bottom; ventral view) is located bilaterally in the posterior to mid-fusiform gyrus, extending also into the occipito-temporal sulcus and is located anterior and lateral to areas v4/v8 (Sereno et al., 1995; DeYoe et al., 1996; Hadjikhani et al., 1998). As can be seen in Fig. 6, pFs/LOa partially overlaps with a face-selective region, called the fusiform face area or FFA (Kanwisher et al., 1997), a topic to which we return later in this review. Although the two subregions of the LOC are anatomically segregated, it is not yet clear whether they are functionally distinct. In some experiments (Grill-Spector et al., 1998a) no functional difference was found between LO and pFs/LOa, while other more sophisticated experiments reveal that the dorsal-caudal region (LO) is sensitive to the location and size of objects, while the ventral-anterior region (LOa/pFs) is not (Grill-Spector et al., 1999).

However, another recent study (Lerner, Hendlar, Harel, & Malach, 2001) suggests that the LOC may be functionally segregated along an anterior-posterior axis, beginning in retinotopic regions (V4/V8) and continuing into the LOC. Lerner et al. (2001) used a scrambling paradigm, in which images were broken into small blocks and then randomly reorganized (see also Grill-Spector et al., 1998b). In different trials, the images were broken into a different number of blocks, ranging from two to 256. They found that in anterior-lateral regions within the LOC, the activation was reduced when images were scrambled into four blocks, while in posterior regions within the LOC the activation was reduced only when images were scrambled into more than 16 blocks. Thus, the anterior-lateral regions were the most sensitive to image scrambling. However, even in anterior regions, activity was not reduced when objects (faces and cars) were cut into halves, either vertically or horizontally. Therefore, neuronal properties appear to progress from a greater sensitivity to local features in retinotopic cortex to more global representations in anterior-lateral regions.

In addition to LO and pFs/LOa, many experiments reveal additional object-selective regions in the dorsal visual pathway (Ungerleider & Mishkin, 1982) Dorsal object-selective foci (Grill-Spector et al., 1998a Grill-Spector et al., 1998b Grill-Spector et al., 2000) include regions that may be partially overlapping V3a, extending into an area immediately anterior to it, possibly V7 (Tootell et al., 1998a). Other non-retinotopic areas that respond more strongly when subjects view intact instead of scrambled objects include regions in the posterior part of the intraparietal sulcus (see also a recent macaque study Sereno & Maunsell, 1998).

3. Cue invariance in the LOC

As mentioned previously, any useful object recognition system should be relatively insensitive to the precise physical cues that define an object and also be relatively invariant to the viewing conditions that affect the object's appearance but not its identity. That is, a good recognition system should have 'perceptual constancy'. For example, one should be able to identify a dog whether it is close or far (i.e. its retinal image either large or small) and whether it is viewed from the front or seen from the side. Also, a dog can be recognized

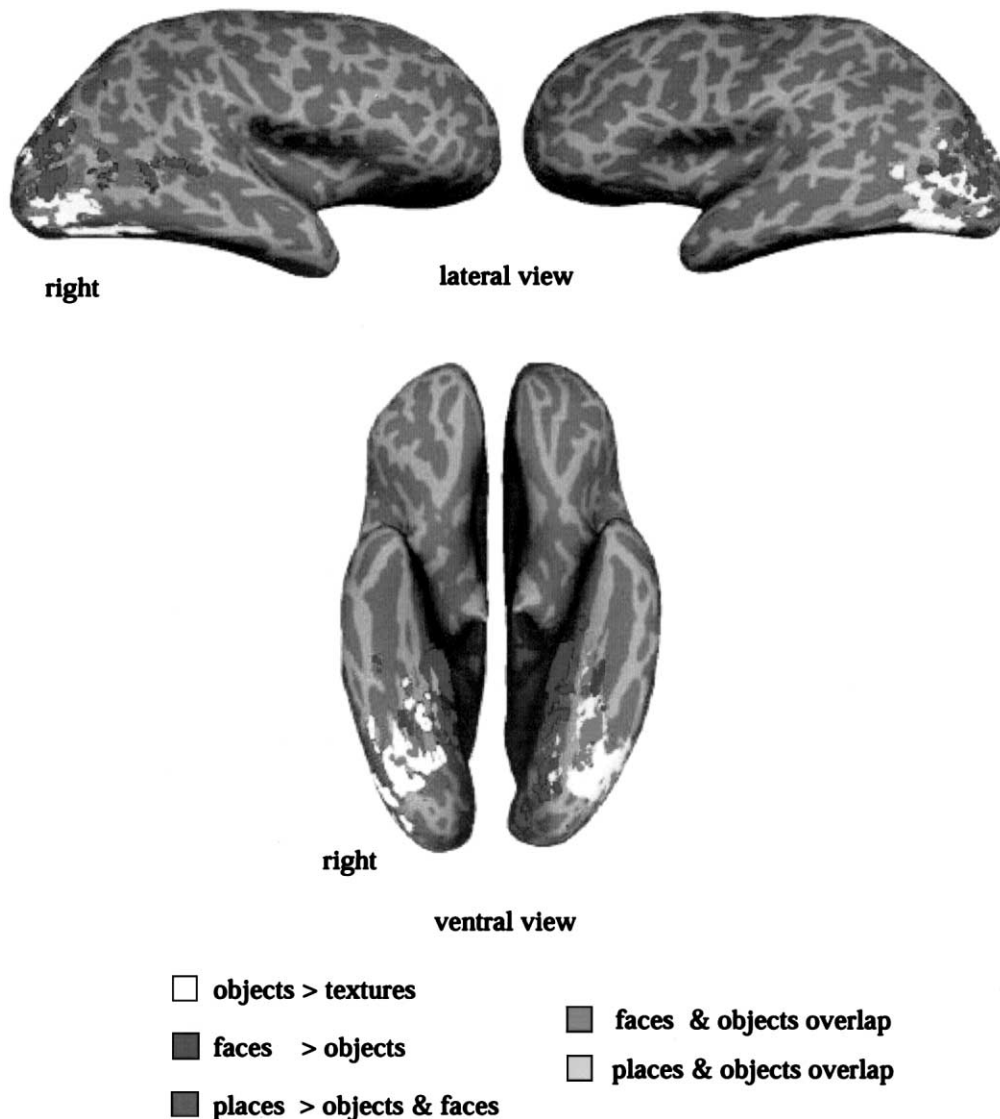


Fig. 6. Object and category-specific regions in the human visual cortex. Object, face and place selective regions depicted on the inflated brain of subject NT. The top panel illustrates the lateral view of the brain and the bottom panel the ventral view. Yellow: object-selective regions were defined by a t -test ($P < 10^{-4}$) that detected regions that were significantly more activated by photographs of cars or abstract sculptures compared to textures. Blue: face-selective region defined by a statistical test that searched for regions activated stronger by faces compared to cars and novel objects. Purple: regions activated more by images of outdoor scenes and houses compared to objects and faces. Green: overlapping regions that were selectively activated both by faces versus objects and objects versus textures. Pink: overlapping regions that respond preferentially both to objects versus textures and places versus objects and faces.

whether it is a real dog, a grayscale photograph or a line drawing. Insensitivity to the specific visual cues that define an object is known as ‘cue-invariance’. In the following section, we will review evidence from recent studies showing that LOC is involved in the representation of shapes rather than the physical properties or local features in the visual stimulus.

Several laboratories have used fMRI to examine human visual areas that exhibit cue-invariance. Grill-Spector et al. (1998a) scanned observers while they passively viewed objects defined by either luminance (objects-from-luminance in Fig. 2a), texture (objects-from-texture in Fig. 2a) or motion cues (random noise object-silhouettes moved against a background of stationary random dots: objects-from-motion in Fig. 2b). Control stimuli consisted of textures, stationary dot patterns or coherently moving dots. LOC and dorsal object-selective foci were more strongly activated by objects compared to control, regardless of the visual cues used to define object shape, confirming cue invariance. In a recent report, Gilaie-Dotan, Ullman, Kushnir, Steinberg and Malach (2000) demonstrated that voxels showing preferential activation to luminance-defined objects were also activated preferentially by stereo-defined objects. Other studies have shown that these regions are also activated when subjects perceived simple shapes that were created via illusory contours, color contrast or stereo cues (Mendola, Dale, Fischl, Liu & Tootell, 1999) and also by texture boundaries (Kastner, De Weerd & Ungerleider, 2000). Kourtzi and Kanwisher (2000a) examined the effect of changing the object format, in particular they tested whether common or different regions in the LOC are involved in the processing of 3D objects depicted either by grayscale photographs of objects or line drawings. They found that the cortical regions that were activated more strongly by gray-level photographs of objects compared to scrambled images were also activated more strongly by line drawings of objects compared to their scrambled controls. Taken together, these results demonstrate convergence of a wide range of unrelated visual cues that convey information about object shape within the same cortical regions, providing strong evidence for the role of the LOC in processing object shape.

However, it is possible that within these object-selective regions, there exist functionally distinct neural populations that are sensitive to different visual cues, but are physically interleaved below the spatial resolution of the fMRI. To test this hypothesis, Kourtzi and Kanwisher (2000a) used an event-related adaptation paradigm (Grill-Spector et al., 1999; Kourtzi & Kanwisher, 2000a) in which they showed subjects pairs of stimuli that appeared sequentially. Stimulus pairs were either of the same or different object, and were either in the same or different format (grayscale vs. line drawing, see Fig. 3). Their results reveal that the fMRI signal in

LOC was reduced (adapted) to the same degree for pairs of identical images and for stimulus pairs in which the same object was shown in different formats. This result demonstrates that neuronal populations within LOC are invariant to the format in which the object was shown and this invariance occurs within neural populations. Thus, these object-selective regions are involved in the representation of object structure, independent of the visual cues that define shape.

Intriguingly, recent evidence suggests that some regions within LO might exhibit not only cue invariance, but also modality-invariance. A recent study (Amedi, Malach, Hendler, Peled & Zohary, 2001) revealed that regions in the vicinity of LO and partially overlapping it, activated more strongly when subjects touched objects, but not when they touched textures. Many voxels in this region also showed greater activation when subjects looked at pictures of objects versus textures. Thus, this region showed selectivity for objects compared to textures in both modalities and may constitute a neural substrate for the convergence of multi-modal object representations.

4. Does the LOC represent contours or shapes?

The studies discussed in the previous section provide evidence that the LOC represents object shape independent of the image features that define that shape. However, they do not enable us to determine whether the LOC processes information about visual contours rather than information about the shape itself. These two hypotheses are difficult to distinguish because contours are always present in images of objects. To test these hypotheses, Kourtzi and Kanwisher (2000b) asked whether adaptation in the LOC would be observed for (a) objects that have the same shape but different contours and (b) objects that have different shape but share the same contours. Adapted responses were observed in the LOC for the same shapes independent of the shape contours. Specifically, when the perceived shape was the same for the two stimuli but the contours were different (because occluding bars occurred in front of the shape in one stimulus and behind the shape in the other), adaptation was as strong as for a pair of identical stimuli. In contrast, when the perceived shapes were different but the contours were identical (because of a stereo-induced figure-ground reversal), no adaptation was found. In another recent study Hasson et al. (2001) used a modified Rubin face–vase illusion in which subjects perceived either a face or a vase. They report that the activation in faces selective regions in the FFA and LO was correlated to times in which subjects reported that they saw a face, but not to times in which they saw a vase, although both the contours and local features were identical.

Overall, these results provide evidence that neural populations in the LOC are involved in processing the shape of objects rather than low level contours.

5. Is information about the 3-D structure of objects processed in the LOC?

Recent human fMRI studies have shown stronger activations into the LOC than in earlier retinotopic regions for 2D shapes defined by stereoscopic depth cues (Mendola et al., 1999) and for curved 3D surfaces defined by coherent motion (Paradis et al., 2000). Moreover, increased neural activity in the LOC has been shown when images of objects are perceived as 3D volumes rather than as 2D shapes (Moore & Engel, 2001). However, other studies (Kourtzi & Kanwisher, 2000a,b; Gilaie-Dotan et al., 2000) suggest that the LOC is not specifically involved in extracting depth information. Further studies are required to test whether depth information per se is coded within LOC or whether depth cues contribute to the perception and processing of shapes and therefore engage the activation of LOC.

Recent monkey physiological studies provide some insights in the processing of depth information about objects. Neurons in the lower bank of the superior temporal sulcus showed selective responses to concave versus convex stereoscopically defined 3D shapes, while neurons in the lateral TE were not selective for 3D shape and showed equal responses to stereoscopically defined shapes and to their monocular images (Janssen, Vogels & Orban, 2000). These results suggest that a possible candidate for selective processing of 3D object structure is the caudal-dorsal subdivision of the LOC or a posterior region in the STS rather than the ventral-anterior part. Furthermore, recent monkey fMRI studies (Serenó, Trinath, Augath, & Logothetis, 2000; Tsao et al., 2000) suggest that 3D shape processing may implicate regions in the inferotemporal cortex, as well as regions involved in motion and depth processing in the dorsal visual stream.

6. Invariances versus sensitivities to object transformations in the LOC

Theories of object recognition most critically differ in their claims about the nature of the representation of objects. Some theories (e.g. Biederman, 1987) suggest a 3D object-centered representation, while other theories posit that multiple 2D views of an object span its representation (e.g. Poggio & Edelman, 1990; Ullman, 1996; Edelman & Duvdevani-Bar, 1997). Physiological studies in macaque IT provide evidence for both viewpoint specific neurons (Perrett, Smith, Potter, Mistlin, Head, Milner & Jeeves, 1985; Logothetis, Pauls &

Poggio, 1995) and viewpoint-invariant neurons (Hasselmo, Rolls, Baylis & Nalwa, 1989; Booth & Rolls, 1998), though the former appears to be more prevalent than the latter.

Previous fMRI studies have found comparable responses for small and large objects in the LOC (Malach et al., 1995) and a comparable fMR signal for frontal and profile views of faces (Tong et al., 2000) in the fusiform gyrus. However, because of the limited spatial resolution of conventional imaging methods, these results could be either due to invariance in the neuronal level or could reflect the averaged response of diverse and noninvariant populations of neurons within each voxel.

Using fMR-adaptation (fMR-A), Grill-Spector et al. (1999) investigated the properties of neuronal populations within the measured voxels, using a variety of objects (animals, man-made objects, faces) and formats (gray-level photos, sketches and line drawings). fMR-A is the phenomenon that high-order cortical regions show a reduction in the fMR signal when presented repeatedly with the same stimulus (e.g. Buckner et al., 1995; Buckner et al., 1998). The neuronal mechanisms underlying this repetition effect are not fully understood, but a straightforward interpretation is neuronal adaptation. Indeed, shape adaptation by repetition has been documented by several studies in macaque IT neurons (e.g. Miller, Li & Desimone, 1991; Ringo, 1996). To test invariance Grill-Spector et al. (1999) measured the extent of fMR-A in the LOC when objects were viewed undergoing only one transformation at a time and keeping the others constant. They reasoned that if the neurons in the LOC were invariant to a particular transformation (e.g. position) they would adapt to repeated presentations of the same objects presented at different locations, in a similar manner to identical repetitions of the same picture. Indeed, Lueschow, Miller and Desimone (1994) have used the neuronal adaptation phenomenon to quantify size and translation invariance of IT neurons. However, if different neurons encode the same object at different locations, then changing the position of the stimulus in the visual field would prevent adaptation.

Grill-Spector et al. (1999) found that different kinds of image transformations produce different levels of adaptation within the LOC. Adaptation in pFs/LOa was found to be largely invariant to size and position (at least in the range of changes tested in the experiment), but not invariant to illumination and viewpoint (see Fig. 4). These results imply that the representation of objects at least in the level of LOa/pFs is view-based rather than based on 3D object representations. These results are also consistent with reports of translation and size invariance in macaque IT by several research groups (Gross et al., 1972; Ito et al., 1994, 1995). The dorsal-caudal subdivision-LO did not show size or position

invariance, although it was adapted by identical images (see Fig. 4). The fact that the more posterior subdivision of the LOC (LO) was still sensitive to size and position changes are consistent with macaque studies suggesting a progression of areas in IT cortex, from TEO or PIT that retains some degree of retinotopy to TE or AIT in which the representations are more invariant. Importantly, these neuronal invariances to changes in size and position should be contrasted with the high degree of shape selectivity in LOC revealed by the relative lack of adaptation in the blocks where objects from the same basic category (i.e. cars or faces) were presented under identical viewing condition (but see Koutstaal et al., 2001, who suggest that there are some occipito-temporal regions that are also adapted by primed but not identical pictures of the same semantic category).

7. From representation to object recognition

In order to link fMRI activation to both neuronal activity and perception, it is crucial to perform parametric experiments that examine the activation of brain regions as a function of some stimulus parameter that is monotonically varied (for a review, see Parker & Newsome, 1998) and that can, in turn, be related to behavior and/or to single-unit recording data. For example, Heeger et al. (2000) showed that contrast tuning in human V1 as revealed by fMRI has a very similar profile to contrast tuning in macaque V1 neurons. Two other recent studies have shown a striking resemblance between the sensitivity of the BOLD signal from human area MT (Heeger, Boynton, Demb, Seidemann, & Newsome, 1999; Rees, Friston, & Koch, 2000) to the tuning of macaque MT cells (e.g. Salzman, Britten, & Newsome, 1990; Britten, Shadlen, Newsome, & Movshon, 1992).

In higher-level visual areas, it is expected that the activation should be less correlated to the low-level features in the visual stimulus and more to perception. Indeed, several studies provide evidence that the activation of the LOC and near-by cortical regions (the FFA and the PPA) is correlated to subjects' perception of objects in a variety of experimental paradigms and tasks (Vanni, Revensou, Saarienen & Hari, 1996; Dolan et al., 1997; Tong, Nakayama, Vaughan & Kanwisher, 1998; Kleinschmidt, Buchel, Zeki & Frackowiak, 1998; George et al., 1999; Grill-Spector et al., 2000; James, Humphrey, Gati, Menon & Goodale, 2000; Doninger et al., 2000; Avidan-Carmel et al., 2000; Bar et al., 2001; Hasson et al., 2001).

Grill-Spector, Kushnir, Hendler, & Malach (2000) demonstrated that there is a correlation between subjects' ability to recognize objects and the activation in the LOC when the exposure duration of masked picktures of objects was varied between 20 and 500 ms.

While, stimulus duration has a relatively small effect on activation in V1, shortening the exposure reduced in a nonlinear manner the activation in the LOC. Further, the curves relating performance and MR signal intensity to stimulus duration were strikingly similar. These results are consistent with a recent physiological study (Keysers, Xiao, Foldiak, & Perrett, 2001) demonstrating that the selectivities of single neurons in the superior temporal sulcus are retained, even at extremely short presentation durations in a fashion comparable to discrimination performance in humans. To further examine the possibility that the reduction of the signal at extremely short duration is related to recognition and not to other factors, Grill-Spector et al. (2000) trained subjects to recognize images presented for 40 ms. After training, subjects' performance increased two-fold on the set of trained images. Importantly, the fMRI signal from the LOC increased for the trained images compared to untrained images shown for the same exposure duration. The high correlation of MR signal intensity in the LOC with recognition argues against the idea that cortical activation is correlated with the effort exerted by subjects in their attempt to recognize objects, since recognition effort should be reduced after training. These results suggest a clear correlation between subjects' recognition performance and selective activation in human object-selective areas.

Similarly, Bar et al. (2001) used an event-related paradigm in which line-drawings of objects were shown briefly and then masked, to find regions that are correlated with an increased perceptual awareness of objects. They report that anterior regions in the fusiform gyrus display stronger activation in trials when subjects report that they have recognized objects compared to trials in which subjects report that they have almost recognized objects.

In another study, James et al. (2000) compared the effect of priming before and after recognition. They used a paradigm in which objects were revealed gradually from behind blinds or through random noise over periods of 45 s. This paradigm stretches the time it takes subjects to recognize objects. In this study, James et al. (2000) found that in both the fusiform gyrus and posterior parietal regions, the fMRI signal increased prior to recognition (with a shorter latency for primed versus unprimed objects), while the fMR signal was reduced after recognition, potentially due to adaptation effects.

The role of the LOC in object recognition has also been tested using a different manipulation: changing the contrast of pictures. Avidan-Carmel et al. (2000) mapped the contrast sensitivity of various human visual areas using fMRI while subjects viewed line drawings of faces and complex objects. While early visual areas showed strong contrast dependence (Boynton, Engel, Glover, & Heeger, 1996; Boynton, Demb, Glover, &

Heeger, 1999) the LOC was essentially invariant to contrast changes between 10 and 100%. Moreover, activation in the LOC matched the recognition performance of the subjects, which reached an asymptote at 10% contrast. When the contrast was reduced below 10%, both psychophysical performance and activity in LOC declined in a similar fashion. Thus, mapping the contrast response function of various visual areas reveals the transition from areas in which activity correlates with the physical properties of the stimulus, to higher order areas in the LOC, in which activity correlates with recognition performance subjects.

Although the results reviewed in this section point to a correlation between the level of recognition performance and signal strength in object-selective regions, it should be emphasized that recognition is not the only factor that determines activity in these areas. Additional factors can modulate the amplitude of fMRI activation even when recognition is maintained. One example is fMR-adaptation, in which the amplitude of the fMR signal in the LOC is reduced due to repeated presentation of the same object (Buckner et al., 1998; Buckner & Koutstaal, 1998; Grill-Spector et al., 1999). Another example is attention, which can increase or decrease responses in most or all visual areas (for a review see Kanwisher & Wojciulik, 2000).

8. Category specific regions of cortex

In this review, we have focused primarily on the LOC, which is defined functionally as the region of occipital and temporal cortex that responds more strongly to objects than to scrambled objects or textures. The LOC has been shown to respond quite strongly and similarly to all kinds of objects tested so far, from cars to novel 3D objects that subjects have never encountered before. As such, the functional properties of the LOC contrast quite sharply with those of two other nearby cortical regions, each of which responds in a much more category-selective fashion: the fusiform face area or FFA (Kanwisher et al., 1997) and the parahippocampal place area or PPA (Epstein & Kanwisher, 1998; Epstein, Harris, Stanley, & Kanwisher, 1999). What is the nature of these category-selective regions of cortex and how are they related functionally and anatomically to the LOC?

The fusiform face area has been studied extensively in many different experiments and laboratories (see Kanwisher, Downing, Epstein and Kourtzi, 2001 for a review). These studies generally agree that the FFA responds much 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) than to various nonface control stimuli (e.g. cars, scrambled faces, houses, hands). The FFA can be found in the vast majority of normal subjects scanned. How-

ever, it is not the only face-selective region in human cortex. In some subjects, face-selective activations can also be found in a more posterior region (Kanwisher et al., 1997) sometimes called the Occipital Face Area (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999) and/or in a region near the posterior end of the superior temporal sulcus (Puce, Allison, Gore, & McCarthy, 1995; Haxby, Hoffman, & Gobbini, 2000).

While the basic response properties of the FFA are generally agreed upon, what they say about the function of this region is considerably less clear. Kanwisher (2000) and others have argued that the FFA is primarily involved in the detection and/or recognition of faces. Indeed, Tong et al. (1998) used binocular rivalry to show that the activation in the FFA is correlated with the perception of a face, while the activation of the PPA is correlated to the perception of a house, even though the retinal stimulation was identical in the two cases. However, an important unresolved question concerns the functional significance of the responses in the FFA to 'non-preferred' stimuli, which are lower than faces, but not zero. The critical question is whether these lower responses reflect a critical involvement of the FFA in the detection or recognition of nonface objects (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Tarr & Gauthier, 2000). Preliminary data from one study (Grill-Spector & Kanwisher, unpublished data) suggest that when stimulus conditions are held constant, activity in the right FFA is correlated with successful detection and recognition of faces, but not with successful detection or recognition of inanimate objects. If this finding is borne out in further studies, it will suggest that the right FFA carries out a critical aspect of the perception of faces, but not of nonfaces.

Another category-selective region of cortex, the PPA (Epstein & Kanwisher, 1998; Aguirre, Zarahn, & D'Esposito, 1998; Epstein et al., 1999) responds strongly to a wide variety of stimuli depicting places and/or spatial layouts (e.g. outdoor and indoor scenes, abstract Lego scenes, and houses) compared to various nonplace control stimuli (e.g. faces, scrambled scenes and Lego objects). Although overall activity in the PPA (like the FFA) can be modulated by attention (O'Craven, Downing, & Kanwisher, 1999; Wojciulik, Kanwisher, & Driver, 1998), the response profile is largely task-independent. Thus, early accounts of PPA function (Epstein & Kanwisher, 1998; Epstein et al., 1999) emphasized perceptual processing of scenes and places. However, the investigation of a neurological patient with no PPA and largely preserved place perception appears to indicate that the PPA may be more critical for encoding scenes into memory than for perceiving them in the first place (Epstein, DeYoe, Press, & Kanwisher, 2001). Numerous questions about the function of the PPA remain. What is clear is that the response in the PPA is very selectively engaged by stimuli that depict places and spatial layouts.

Anatomically, the PPA is clearly distinct from the LOC (purple in Fig. 6). However the FFA is close to and partially overlapping with the anterior part of the LOC (blue and green in Fig. 6). 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) and 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 uniquely categorize each region of cortex, posing some challenges of interpretation. One rather extreme account of this situation is that the FFA 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, Tanaka, Ito, & Cheng, 1992) at such a fine scale that they cannot be resolved with fMRI, except for a few very large regions such as the FFA. Another possibility is that the FFA and the LOC are actually anatomically non-overlapping, but that limitations in the spatial resolution of fMRI lead to spurious overlap. Further research will be needed to resolve this question.

How many such category-selective regions of cortex exist in the human visual pathway? Other categories have been reported to selectively activate focal regions of cortex, including animals, tools (Martin, Wiggs, Ungerleider, & Haxby, 1996; Chao, Haxby et al., 1999) and letter strings (Allison et al., 1994b). However, the evidence is not as clear in these cases. Indeed, ongoing work in our laboratory (Downing & Kanwisher, unpublished data) suggests there may be very few regions of cortex that exhibit the kind of strong category selectivity that is found in virtually every subject for faces (in the FFA) and places (in the PPA).

Thus, it appears that the ventral visual pathway contains one region, the LOC, which exhibits little selectivity for specific object categories and in addition, there exist a small number of category-specific modules (for faces, places and perhaps one or two others yet to be discovered). Indeed, it would seem a sensible design for the cortex to supplement its general-purpose mechanism for describing the shape of any kind of visually-presented object (i.e. 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. However, the lack of evidence for category specific mechanisms within the LOC could be also due to the limited spatial resolution of fMRI. Finally, another (nonexclusive) possibility is that each object is represented as the entire pattern of activity across all of these regions (LOC, FFA, PPA) and that it is this distributed representation that forms the basis of object recognition (Edelman et al., 1998).

9. Conclusions

The studies discussed above shed light on two of the central issues in object recognition: the nature of the representations mediating recognition and the functional architecture of the system that carries it out. We have focused on the lateral occipital complex, a large cortical region that appears to play a central role in object recognition. Data from several laboratories indicate that activity in the LOC is correlated with behavioral performance on a variety of different object recognition tasks and for a wide variety of types of stimuli. In this sense, the LOC appears to be a kind of general-purpose system for analyzing object shape, in contrast to other cortical regions such as the FFA and PPA that are more selectively engaged by particular stimulus classes. However, while the activation of each of these regions has been linked to the ability of subjects to recognize stimuli of various kinds, the precise nature of the processes that go on in each of these high-level regions remains controversial (e.g. Gauthier et al., 1997; Op de Beeck, Beatse, Wagemans, Sunaert, & Van Hecke, 2000; Tarr & Gauthier, 2000).

Given its central involvement in object recognition, we can expect an investigation of the LOC to be informative about the nature of the representations involved in recognition. Substantial evidence indicates that the LOC represents the shapes of objects independent of the low-level visual cues (e.g. color, motion, texture) that define those shapes. Additional experiments suggest that the LOC might contain a hierarchy of shape-selective regions with more posterior regions activated also by object fragments while anterior regions exhibit stronger activation for whole or half objects. Further, the representations underlying object recognition appear to be invariant to some degree to changes in size and position, yet specific to the direction of illumination and the viewpoint of the object.

In sum, the findings reviewed here suggest that object recognition is accomplished by the operation of both category-specific and general-purpose mechanisms. The results reviewed here indicate that fMRI is already beginning to provide important insights about how humans recognize objects. We expect that this trend will only increase in the future.

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