

THE HUMAN VISUAL CORTEX

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Key Words functional magnetic resonance imaging (fMRI), visual perception, object and face recognition, retinotopic mapping

■ **Abstract** The discovery and analysis of cortical visual areas is a major accomplishment of visual neuroscience. In the past decade the use of noninvasive functional imaging, particularly functional magnetic resonance imaging (fMRI), has dramatically increased our detailed knowledge of the functional organization of the human visual cortex and its relation to visual perception. The fMRI method offers a major advantage over other techniques applied in neuroscience by providing a large-scale neuroanatomical perspective that stems from its ability to image the entire brain essentially at once. This bird's eye view has the potential to reveal large-scale principles within the very complex plethora of visual areas. Thus, it could arrange the entire constellation of human visual areas in a unified functional organizational framework. Here we review recent findings and methods employed to uncover the functional properties of the human visual cortex focusing on two themes: functional specialization and hierarchical processing.

INTRODUCTION

In the past decade the use of noninvasive functional imaging, particularly functional magnetic resonance imaging (fMRI), has dramatically increased our detailed knowledge of the functional organization of the human visual cortex. Thus, more than a dozen putative human visual areas have been described using fMRI (Tootell 1996, 2003). The discovery and analysis of cortical visual areas are major accomplishments in visual neuroscience. The number, locations, and functional roles of these areas are important topics for continuing experimental studies of the human brain.

In trying to account for the multiplicity of visual areas, two main principles have been suggested: hierarchical processing and functional specialization. Hierarchical processing proposes that visual perception is achieved via a gradual stagewise process in which information is first represented in a localized and simple form and, through a sequence of processes, is transformed into more

abstract, holistic, and even multimodal representations (DeYoe & Van Essen 1988). The second principle, functional specialization, proposes that specialized neural pathways exist that process information about different aspects of the visual scene. In particular the visual system may consist of parallel hierarchical sequences, or processing streams, that are specialized for a particular functional task. The dorsal stream, also referred to as the “where” (Mishkin et al. 1983) or “action” (Goodale et al. 1991) stream, has been associated with spatial localization (or visually guided action) and the ventral “what” stream (Mishkin et al. 1983), which are involved in object and form recognition and are the best-known of the processing streams.

Here we review recent findings and methods employed to uncover the functional properties of the human visual cortex, focusing on these two themes: functional specialization and hierarchical processing.

MAPPING THE HUMAN VISUAL CORTEX

In the macaque, visual cortical areas have been distinguished by four main criteria (Felleman & Van Essen 1991, Tootell et al. 2003): (*a*) retinotopy, (*b*) global functional properties, (*c*) histology, and (*d*) intercortical connections. In humans, most visual cortical areas have been revealed by functional MRI, using retinotopic and global functional criteria. Several studies explored histological differences between human brain areas on postmortem specimens, but these have been largely restricted to early visual areas (Clarke 1994a,b; Horton et al. 1990; Horton & Hedley-Whyte 1984; Tootell & Taylor 1995). More recently, anatomical MRI and diffusion tensor imaging (DTI) have revealed histological and connectional distinctions between areas as well (Conturo et al. 1999, Hagmann et al. 2003). We begin by reviewing methods applied most commonly to delineate visual areas: retinotopy and functional specialization.

PRINCIPLES OF RETINOTOPIC MAPPING

Visual field topography is used to identify and map visual areas in animals and humans (DeYoe et al. 1996; Engel et al. 1994, 1997b; Sereno et al. 1995, 2001; Wandell 1999a). Mapping from the retina to the primary visual cortex is topographic in that nearby regions on the retina project to nearby cortical regions. In the cortex, neighboring positions in the visual field are represented by groups of neurons adjacent but laterally displaced within the cortical gray matter. Mapping between the retina and the cortex can be described best as a log-polar transformation, in which standard axes in the retina are transformed into polar axes in the cortex: eccentricity (distance from fovea) and polar angle (angle from horizontal axis; see Figure 1). The logarithmic component of the transformation accounts for the magnification of central representations in the cortex

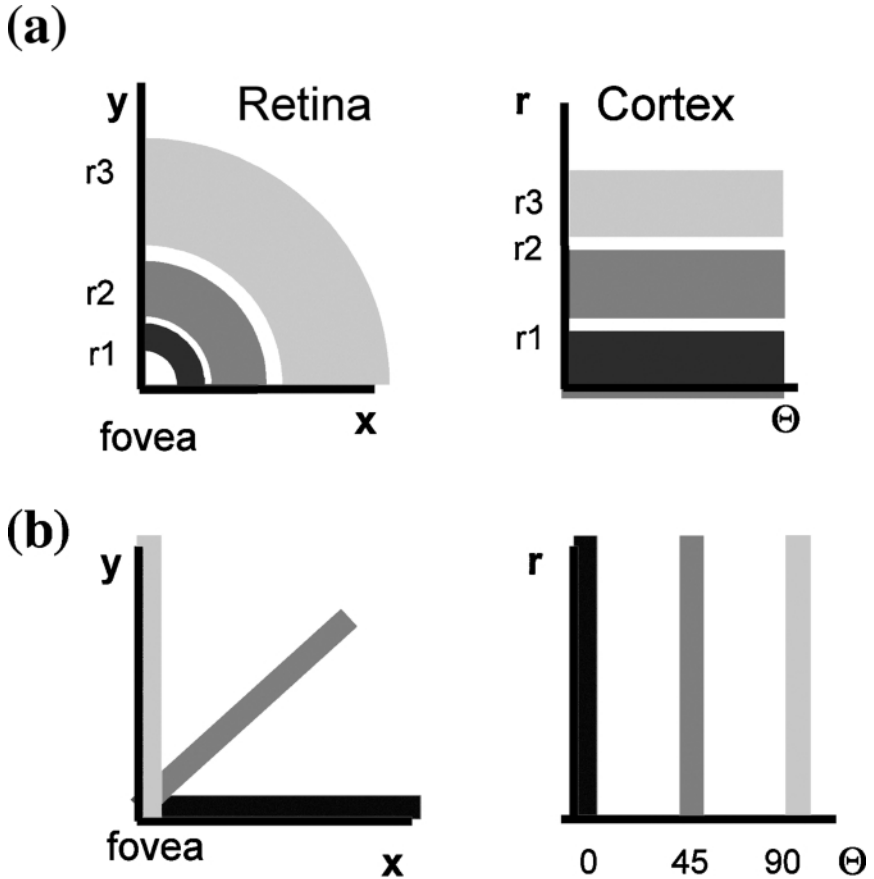


Figure 1 Principles of retinotopic mapping. Log-polar transformation from retinotopic coordinates to cortical coordinates. (A) Eccentricity: distance from the fovea. (B) Phase: polar angle from the horizontal.

(Duncan & Boynton 2003, Schwartz et al. 1985). Thus, this transformation from retina to cortex preserves the qualitative spatial relations but distorts quantitative ones.

Topographical cortical representations are revealed when subjects fixate and visual stimuli are presented at selected locations. Mapping the phase (angle) component of the retinotopic map reveals multiple horizontal and vertical meridian representations arranged in approximately parallel bands along the cortical surface (Figure 2). These vertical and horizontal meridian representations alternate and define the borders between mirror-symmetric retinotopic areas. Perpendicular to these bands lie iso-eccentricity bands, which constitute an eccentricity

gradient (Figure 3). However, the representation of the fovea is greatly expanded compared to the representation of the periphery. In humans the foveal representation of low-level retinotopic areas converges in the occipital pole, in the confluent fovea (black arrows in Figure 3). Flanking the confluent fovea there are bands of parafoveal and peripheral representations present both ventrally and dorsally.

By using stimuli that are more optimal for activating mid- and high-level visual areas (Grill-Spector et al. 1998a,b; Hasson et al. 2003a,b; Levy et al. 2001), we revealed consistent retinotopic maps in what is classically regarded “nonretinotopic cortex.” Specifically, orderly central and peripheral representations can be found all across visual cortex, extending (albeit with decreased precision) even into high-level regions presumably engaged in face and place perception. Whereas the polar angle maps decline faster than eccentricity maps, replicable polar representations also extend more anteriorly and laterally than initially thought. This finding implies that to subdivide visual cortex into areas that are retinotopic versus nonretinotopic may be oversimplistic. This distinction now appears to be a continuum, not a dichotomy. We are hopeful that these consistent retinotopic representations will be used, in addition to functional specialization, to systematically delineate high-level visual areas.

EARLY VISUAL AREAS

Each retinotopic visual area contains a complete eccentricity and polar angle map (DeYoe et al. 1996, Sereno et al. 1995). On the unfolded cortex, phase lines lie approximately orthogonal to eccentricity bands and provide a one-to-one mapping of visual space in cortical coordinates (Figure 4). The details of the anatomic locations of different retinotopic visual areas have been described in detail recently (Wandell 1999a). Here we note that on the unfolded cortical hemisphere, early retinotopic areas V1, V2, V3, V4/V8, and V3a are arranged as parallel, mirror-symmetric bands.

In the dorsal stream, beyond area V3a investigators have identified three additional visual retinotopic areas. However, a consensus has yet to emerge regarding their exact parcellation. Area V7 contains an additional hemifield representation anterior to V3a (Press et al. 2001). V7 horizontal and vertical meridians are rotated compared to V3a meridians (Figure 4). This area may have a separate fovea located along the intraparietal sulcus (IPS) (Press et al. 2001). Others (Press et al. 2001, Smith et al. 1998) have defined another hemifield representation lateral and inferior to V3a, termed V3b. This area shares a parafoveal representation with V3a. Recently, Sereno and colleagues (Sereno et al. 2001) reported yet another hemifield representation more anteriorly along the intraparietal sulcus, which shows robust topographic mapping of a remembered target angle. Sereno and colleagues suggested that this region may correspond to the lateral intraparietal (LIP) area in macaque monkeys, and they named it hLIP.

FUNCTIONAL SUBSYSTEMS: COLOR, MOTION, DEPTH, AND FORM PROCESSING IN THE HUMAN VISUAL CORTEX

A further possible relation between anatomical structure and physiological maps is the suggestion that there are separate neural pathways for processing information about different visual properties such as motion, depth, color, and shape. Physiological and anatomical studies in the monkey reveal such segregation that begins already at the retinal level of neural pathways (Amir et al. 1993, DeYoe & Van Essen 1988, Shipp & Zeki 1985), and they show some functional compartmentalization throughout visual cortex. However, other studies suggest that this compartmentalization is too simplistic (Malach 1994, Schiller 1996). In the next section we review the current knowledge about processing that leads to the perception of motion, depth, color, and form in the human brain.

The Human “Color Center” and Areas V4/V8

In ventral cortex the border between V3v and V4v is defined by an upper vertical meridian. Currently there is vigorous debate about the functional organization and naming conventions beyond V4v (Bartels & Zeki 2000, Hadjikhani et al. 1998, Tootell et al. 2003, Wade et al. 2002, Wandell 1999b, Zeki et al. 1991) and specifically what constitutes the anterior border of V4. The question is whether V4 ends prior to the lower-field representation (Figure 4), leaving area V4v without its corresponding V4d (Serenio et al. 1995), or whether the lower visual field representation lateral to V4v constitutes V4d, thus, forming a complete hemifield representation, complementary to the dorsal V3a representation (Kastner et al. 2001, McKeefry & Zeki 1997, Wade et al. 2002). In contrast, Tootell and colleagues suggest that on the ventral aspect there is a quarter field representation, V4v, and that the neighboring cortex belongs to a separate area termed V8, consisting of a hemifield representation (Hadjikhani et al. 1998), which is rotated relative to V4v.

The debate about the precise definition of V4 is related to the controversy about the location of a color center in the human brain. Clinical studies reveal that color vision loss (achromatopsia) is correlated with damage in ventral occipitotemporal cortex (Damasio 1980, Pearlman 1979, Zeki 1990), suggesting the existence of a color center in the human brain. Indeed, neuroimaging studies reveal regions in ventral visual cortex in the vicinity of V4v that respond more strongly to colored patterns compared to luminance-defined patterns. These regions are referred to as V4 (Bartels & Zeki 2000, Lueck et al. 1989, McKeefry & Zeki 1997), V8 (Hadjikhani et al. 1998, Tootell & Hadjikhani 2000), and sometimes VO (Wandell 1999b). More anteriorly, investigators found additional areas that were activated by attention to color (Bartels & Zeki 2000, Beauchamp et al. 1999).

The controversy of the functional definition of human area V4 illustrates the need for additional dimensions such as histology (Clarke et al. 1994a,b; Tootell & Taylor 1995) and fiber connectivity (Conturo et al. 1999, Hagmann et al. 2003,

Horton & Hocking 1996) that should be supplemented in the attempts to define areas in the human visual cortex systematically.

Whether or not V4 or V8 is principally a color computation center is an open question. Engel et al. (1997a) measured the responses of area V1 to calibrated color stimuli and showed stronger activation per unit of cone contrast for opponent color stimuli than for pure luminance stimuli. On the basis of a definition that uses the criterion, "responds better to color than luminance," it seems that even striate cortex could be a color area. So too could be the central retina. In studies of the effects of color adaptation, an essential part of color constancy, Wade & Wandell (2002) found that much of the computation can be explained by gain changes in retinal photoreceptors. Thus, until the computational basis of human color vision is understood more clearly, it may be more productive to speak of a color-processing stream that begins in the retina and passes through V1, V2, and higher areas including the V4/V8 complex. Each area contributes to color perception (and to other facets of vision), and their precise functions await a more complete characterization.

Motion Perception

Motion processing encompasses different kinds of information such as the derivation of the speed and direction of a moving target, the motion boundaries associated with an object, or judgment of motion direction from optic flow signals. Along the dorsal stream many regions are activated more strongly when subjects view moving versus stationary stimuli. Included are areas MT, MST, V3a, and even low-level areas such as V1 and V2. However, converging evidence suggests that some aspects of motion processing are localized in more specialized regions in the human brain.

A central motion selective focus in the human brain is a region called hMT+, located at the temporo-parietal occipital junction (Figure 4) (Tootell et al. 1995b, Watson et al. 1993). This region is a likely homologue to the macaque motion-sensitive area called MT/V5 (Heeger et al. 2000, Rees et al. 2000). Human MT+ is selectively activated by moving versus stationary stimuli and exhibits high contrast sensitivity. This area contains an orderly eccentricity organization within a hemifield representation (Dukelow et al. 2001, Huk et al. 2002). Recently, several elegant studies used the perceptual illusion of the motion aftereffect to show that hMT+ probably contains direction-selective neural populations (Huk et al. 2001, Tootell et al. 1995a), similar to findings in macaques (Britten et al. 1992, Maunsell & Newsome 1987, Salzman et al. 1992). Furthermore, comparison of coherent versus incoherent motion of light points (in which dots move independently) reveals a significant change in activation within hMT+ that increases linearly with the coherence of motion but shows little change in early visual areas (Rees et al. 2000). Similarly, hMT+ adapts to patterned motion, in contrast to lower visual areas, which adapt to component motion (Huk & Heeger 2002). These results are consistent with the idea of local motion processing in early visual areas and global

motion processing in later areas (see also Castelo-Branco et al. 2002). Finally, activation of this area is enhanced when subjects attend to or track motion (Buchel et al. 1998, Culham et al. 1998).

Thus, converging evidence shows that human MT+ response properties parallel both the response properties of single neurons (Rees et al. 2000) and perception (Muckli et al. 2002). This inference is further supported by clinical studies that reveal that akinetopsia (the failure to perceive motion) is associated with lesions in the vicinity of hMT+.

In addition to hMT+, other cortical sites are activated by various types of coherent motion stimuli. Some evidence supports the idea that within the hMT+ complex of areas some subregions show selectivity to particular radial and circular motion patterns (rather than simple translation) and thus may be involved in calculating optical flow (Morrone et al. 2000). Orban and colleagues have suggested the existence of yet another specialized motion-related area, the kinetic-occipital area (KO) (Dupont et al. 1997, Van Oostende et al. 1997), which specializes in processing kinetic boundaries created by discontinuities in motion direction (but see Zeki et al. 2003).

Another intriguing aspect of motion processing is related to the perception of biological motion, the motion of people and animals. One of the striking features of motion perception is that humans can differentiate biological motion, such as the types of motion (running, jumping) and even gender of the actor, from extremely impoverished visual displays in which only a dozen light-points are attached to joints of a person moving in an otherwise dark room. Increasing evidence supports an area specialized for perceiving biological motion. This area is located within a small region on the ventral bank of the occipital extent of the superior-temporal sulcus (STS), located lateral and anterior to human MT/MST, and is selectively activated during viewing of light-point-defined moving figures (Grossman et al. 2000, Grossman & Blake 2002, Vaina et al. 2001), but not by the random movement or inverted motion of the same dots that composed the light-point figures. This region is also activated by other types of biological motion such as movies of people walking (Pelphrey et al. 2003) or of hand, eye, or mouth movements (Puce & Perrett 2003). Particularly interesting is the recent association of these regions with the cortical "mirror" system, which integrates both sensory processing and production of motor movements (see Rizzolatti & Craighero 2004, in this volume).

Depth Perception

Compared to the work on motion and form processing there are fewer studies concerning the processing of depth, surfaces (Stanley & Rubin 2003), and three-dimensional structure (Kourtzi et al. 2003a, Moore & Engel 2001). Like the processing of visual motion, the analysis of depth can involve both low-level cues, such as disparity, derived from the retinal images, and high-level inferred attributes, such as the surfaces corresponding to retinal points with different disparities. In

humans, experiments using random dot stereograms have shown a stream of areas that respond to these three-dimensional cues: V1, V2, V3, VP, V3a, and hMT+. Of these areas V3a is the region most sensitive to changes in the disparity range, although all the regions activated by random dot stereograms show a correlation between the amplitude of the fMRI signal and disparity (Backus et al. 2001). In contrast, other high-level areas such as the lateral occipital complex (LOC) respond to random dot stereograms only when these stimuli are used to define object form (Gilaie-Dotan et al. 2002, Kourtzi & Kanwisher 2001a), but these regions do not seem to carry disparity or depth information per se.

OBJECT-SELECTIVE AREAS IN THE HUMAN BRAIN

One of the greatest mysteries in vision research is how humans recognize visually presented objects with high accuracy and speed (Thorpe et al. 1996), despite drastic changes in the appearance of objects caused by changes in the viewing conditions. Interest in how human object recognition works is heightened by the fact that efforts to duplicate this ability in machines have not met extraordinary success. Object-selective regions (Figure 5) respond more strongly when subjects view pictures of objects than textures, visual noise, scrambled objects, or scrambled Fourier phase information (which maintains the spatial frequency spectrum) (Grill-Spector et al. 1998b, Malach et al. 1995). These regions compose a large constellation of areas in both the ventral and dorsal visual pathways that lie anterior and lateral to early retinotopic cortex (Figure 5). We discuss the organization of these areas in terms of three main subdivisions: lateral occipital complex (LOC), ventral occipito-temporal (VOT) regions, and dorsal foci.

A central complex of object-selective activation (including faces) occurs in the lateral occipital cortex. These regions show a greater fMRI response to images of familiar and unfamiliar objects, compared with nonobject controls (Grill-Spector et al. 2001, Kanwisher et al. 1996, Malach et al. 1995). The LOC can be divided into at least two putative subdivisions: a dorsal region [LO (lateral occipital)] and a more ventral region [pFus (posterior fusiform)], along the posterior fusiform gyrus, which may show some overlap with the ventrally located VOT.

Ventrally, a set of regions highly selective to object, face (Kanwisher et al. 1997), and place images (Epstein & Kanwisher 1998) have been described in a stretch of cortex bounded by the fusiform gyrus laterally and the parahippocampal gyrus medially (Ishai et al. 1999, Levy et al. 2001, Malach et al. 2002). Here we refer to these more anterior and ventral regions as ventral occipito-temporal or VOT (Figure 6). Within the VOT, regions that prefer faces (compared to objects and places) manifest a foveal bias, and regions that respond more strongly to houses and scenes show a peripheral field bias (Hasson et al. 2002, 2003a; Levy et al. 2001, 2004; Malach et al. 2002). Kanwisher and colleagues labeled ventral face-selective regions in the fusiform gyrus as FFA [fusiform face area (Kanwisher et al. 1997)] and place-selective regions as PPA [parahippocampal place area (Epstein & Kanwisher 1998)].

Although object-related activation is commonly associated with ventral-stream areas and object recognition, object and shape information also is necessary in a variety of dorsal stream-related tasks, particularly in the context of object manipulation (Culham et al. 2003, Goodale et al. 1991). Thus, it is not surprising that several regions that respond more strongly to objects than nonobject controls have been found dorsally both in the parietal lobe and in the dorsal aspect of the LOC (Figure 6). Although these regions require more rigorous mapping, there are at least two dorsal foci that activate more strongly when subjects view pictures of objects than when viewing faces or scenes: One focus is located inferior and lateral to V3a (Grill-Spector 2003b, Hasson et al. 2003a), and another focus is located anterior to V3a, partially overlapping V7 (Grill-Spector 2003b). Finally, a region that activates more strongly when subjects look at buildings and scenes (compared to objects and faces) and overlaps with peripheral representations is found dorsally along the transverse occipital sulcus (TOS) (Hasson et al. 2003a). The functional role and involvement of dorsal object-selective regions in perceptual tasks are still poorly understood.

REPRESENTATION OF OBJECTS IN HIGH-LEVEL VISUAL AREAS

Many studies have shown that the activation in object-selective cortex exhibits perceptual invariance; object-selective regions in the ventral stream are activated when subjects view objects defined by luminance (Grill-Spector et al. 1998a), texture (Grill-Spector et al. 1998a, Kastner et al. 2000), motion (Grill-Spector et al. 1998a, Kriegeskorte et al. 2003), or stereo cues (Gilaie-Dotan et al. 2002, Kourtzi & Kanwisher 2001a) but not when subjects view textures, stationary dot patterns, coherently moving dots, or gratings defined by either motion or stereo. Other studies have shown that activation is independent of object format [gray scale or line drawing (Ishai et al. 2000)] and that these regions are also activated when subjects perceived simple shapes created via illusory contours (Kourtzi & Kanwisher 2000, Mendola 1999, Stanley & Rubin 2003). Several recent studies indicate that object-selective regions in the ventral stream represent shapes rather than contours or object features (Andrews et al. 2002, Kourtzi & Kanwisher 2001b, Lerner et al. 2002). Using the well-known Rubin vase-face illusion, Hasson and colleagues (Hasson et al. 2001) and Andrews and colleagues (Andrews et al. 2002) demonstrated that face-selective regions in LO and VOT do not represent local contours or local features, since in both areas the activity was significantly correlated with the percept of a face and uncorrelated with local image features. Interestingly, some regions within LO even show cross-modality convergence, activating more strongly to objects than textures for both visually and haptically sensed objects (Amedi et al. 2001, James et al. 2002b).

Furthermore, to be effective, the object-recognition system must be invariant to external viewing conditions that affect objects' appearance but not their identity.

We have previously shown, using the adaptation paradigm (Grill-Spector et al. 1999, 2001), that regions in the OTS and fusiform gyrus (but not LO) indeed show size and position invariance (Grill-Spector et al. 1999). Interestingly, while at the behavioral level, subjects exhibit viewpoint invariance and invariance to the illumination of objects; at the level of VOT we found that object representations are more sensitive to the viewing angle and direction of illumination (Grill-Spector et al. 1999). Two recent studies (James et al. 2002a, Vuilleumier et al. 2002b) show some degree of viewpoint invariance for the representation of objects in VOT when using small rotation angles.

Taken together, these results demonstrate convergence of a wide range of invariances to visual cues and object transformation within the same cortical regions, which supports the role of occipito-temporal object areas in processing object shape.

THE ROLE OF OBJECT-SELECTIVE REGIONS IN OBJECT RECOGNITION

The strong activation of occipito-temporal object-selective regions when subjects view pictures of objects and have a large degree of perceptual constancy does not by itself prove that this region 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 the site of object recognition. Activation during object viewing could be due to other processes, such as visual attention, arousal, figure-ground segmentation, and surface extraction. However, several recent studies show that the activation in ventral (but not dorsal) object-selective areas is correlated to object perception rather than to the low-level features in the visual stimulus.

Experiments in which researchers manipulated a stimulus such that it degraded recognition performance demonstrated the correlation between perception and brain activation in lateral and ventral object areas. Examples include using backward masking and shortening the duration for which pictures of objects were shown (Grill-Spector et al. 2000, see also Figure 11), decreasing the amount of the object that was visible by presenting it behind occluding binds (James et al. 2000), reducing objects' contrast (Avidan et al. 2002a), or presenting letter and objects embedded in noise (Kleinschmidt et al. 2002, Malach et al. 1995). Together, these studies demonstrate that the strength of activation in object-selective regions is lower compared to recognition, and the level of activation increases nonlinearly at recognition threshold.

Other experiments used bistable phenomena such as binocular rivalry (Tong et al. 1998), the Rubin face-vase illusion (Andrews et al. 2002, Hasson et al. 2001), and ambiguous figures to track changes in brain activation that correlate with different perceptual states. The advantage of bistable phenomena is that the percept changes while the physical stimulus remains unchanged. In these studies when subjects perceived a face there was higher activation in face-selective regions

in the fusiform gyrus compared to states in which the stimulus was not perceived as a face.

A different approach is to show pictures close to threshold and compare brain activation in trials in which subjects recognized objects to activation in trials in which objects were present but not recognized (Bar et al. 2001; Grill-Spector 2003a, 2004). These experiments revealed that activation in object and face selective areas is correlated with subjects' perceptual reports rather than with the physical presence of the stimulus (Grill-Spector 2003a). Thus, activation in object-selective cortex was highest when a target face (or object) was identified (identification hit), intermediate when it was detected but not identified (detection hit), and lowest when a target was present but not detected (detection miss) (see Figure 7). Importantly, we also showed that false identifications were correlated with a higher signal than identification misses (Grill-Spector 2003a, 2004). In contrast, lower-level visual areas were activated robustly, but their levels of activation were not correlated with subjects' percepts (Figure 7). In sum, activity in early and intermediate visual areas (e.g., V1 and V4, respectively) correlates with the physical properties of the retinal image, but activity in higher-level areas (e.g., LO and FFA) correlates with subjects' percepts in tasks requiring face and object recognition.

PARCELLATION OF OBJECT-SELECTIVE REGIONS TO FUNCTIONAL SUBDIVISIONS

The parcellation of higher-level regions into visual areas becomes difficult because these regions lack the precise retinotopy of early visual areas, and further, different types of objects activate somewhat different regions within this constellation of regions (Figure 6 and 8). Several research groups noted regions that show strong activations to specific object categories such as faces (Allison et al. 1994, Ishai et al. 1999, Kanwisher et al. 1997, Levy et al. 2001, Puce et al. 1995), animals (Chao et al. 1999, Martin et al. 1996), body parts (Downing et al. 2001, Grossman & Blake 2002), tools (Beauchamp et al. 2002, Chao et al. 1999, Martin et al. 1996), places or houses (Aguirre et al. 1998, Epstein & Kanwisher 1998, Ishai et al. 1999), and letter strings (Cohen et al. 2000, Hasson et al. 2002). These results are summarized in Figure 8. Importantly, the object-selective patterns of activation across occipito-temporal cortex (e.g., faces and houses) are replicable within and across subjects (Levy et al. 2001, Malach et al. 2002). Still unanswered is whether regions that show preference for an object category should be treated as an independent module for processing that category (see below).

At a higher spatial resolution, possibly at a columnar resolution, there may be additional modular representations at a smaller spatial scale, which can be revealed only with higher-resolution imaging or through indirect methods such as fMR-adaptation (Avidan et al. 2002b, Grill-Spector & Malach 2001).

The parcellation of object cortex to functional subdivisions is still unclear. The debate is centered on which functional criteria should be used to partition this

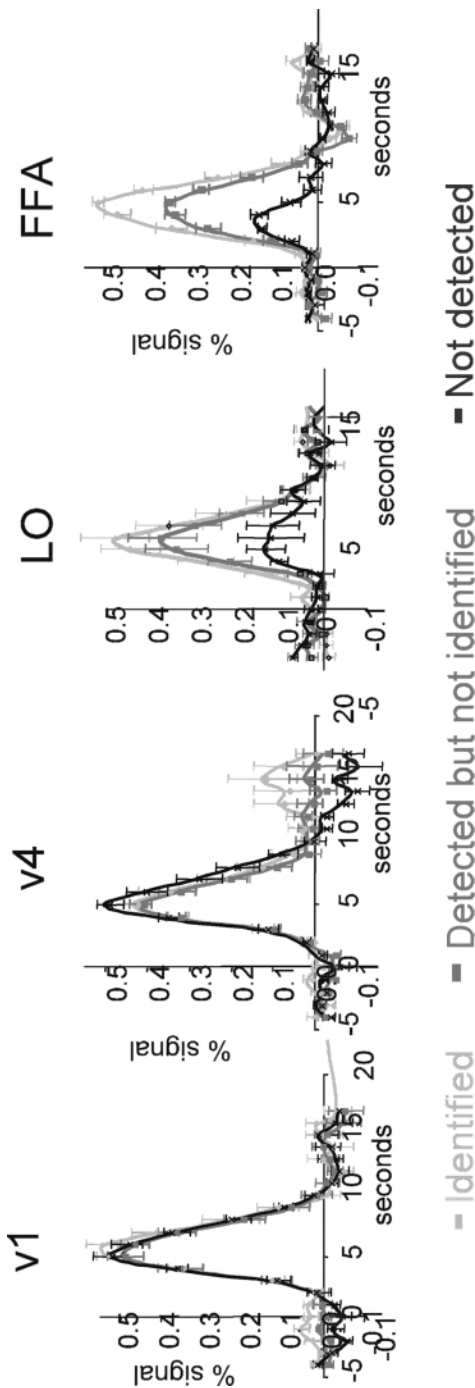


Figure 7 Activation along the ventral visual pathway in a task in which subjects' ability to detect and identify faces was monitored. Shown are time courses of activation in an event-related experiment in which subjects were briefly presented for 33 ms with a displayed picture that was subsequently masked by a texture pattern. Subjects were required to report when they identified a target face, detected a face, or did not detect a face. Here we present the activation pattern for trials in which the target face was presented as a function of subjects' responses. Signal is calculated relative to a fixation baseline (details in Grill-Spector 2003a). Early visual areas are significantly active during this task, but their activation is not correlated with face detection or identification success. In contrast, activation in regions in LO that respond strongly to faces compared to objects and the fusiform face area (FFA) is strongly correlated with subjects' ability to detect and identify faces.

large cortical expanse. At one end of the spectrum is the hypothesis that the whole constellation of regions anterior and lateral to classic retinotopic cortex is one distributed system for object recognition (Haxby et al. 2001, Ishai et al. 1999). At the other end is the hypothesis, proposed by Kanwisher and colleagues, that the constellation of regions in the ventral stream consists of a few domain-specific modules (Kanwisher 2000, Spiridon & Kanwisher 2002) for faces (Kanwisher et al. 1997), body parts (Downing et al. 2001), and places (Epstein & Kanwisher 1998), and the rest is a general purpose object-recognition system. A third hypothesis suggests that occipito-temporal regions should be subdivided on the basis of the semantic attributes of object categories (Chao et al. 1999 Beauchamp et al. 2002). A fourth hypothesis, held by Tarr & Gauthier (2000) suggests that object representations are clustered according to the type of processing required rather than according to their visual attributes. Specifically, Tarr & Gauthier suggest that face-selective regions are engaged in fine-grained discrimination between objects of the same category that is automated by expertise. According to this view, activity in these regions reflects expertise in recognizing certain object categories and is not restricted to faces. Finally, another hypothesis, proposed by Malach and colleagues (Hasson et al. 2003a, Levy et al. 2001, Malach et al. 2002), argues that cortical topography, in particular eccentricity mapping, is the underlying principle of the organization of ventral and dorsal stream object areas. These authors proposed that correlation between regions that prefer faces and central representation and regions that prefer buildings and peripheral representations reflects the basic visual specialization in which different spatial resolutions (cortical magnification factors) are related to different eccentricity bands (which continues into higher-order areas).

These different (but not necessarily contradictory) views emphasize criteria to differentiate between regions involved in object, face, and place perception. Here we propose an alternative framework to examine the human object recognition system as a hierarchical system. The underlying idea implies that object recognition is implemented in the brain through a series of processing stages, in which more global and invariant representations emerge up the hierarchy of the processing stream. The hierarchy is implemented through a gradual transition, from local representations that are closely tied to the retinal image to abstract representations that are closely linked to perception. In the next sections we consider the process of object recognition in the context of a hierarchical processing stream, emphasizing the different types of processing in lower- versus higher-level visual areas in the ventral stream.

FUNCTIONAL MANIFESTATIONS OF HIERARCHICAL PROCESSING IN THE HUMAN VENTRAL STREAM CORTEX

According to hierarchical framework, areas along both the occipito-temporal and occipito-parietal pathways are organized hierarchically, such that low-level inputs are transformed into more abstract representations through successive stages of

processing. Virtually all visual-processing tasks activate V1 and V2. However, as one proceeds from one area to the next the neuronal response properties become increasingly complex. In monkeys, along the occipito-temporal pathway for example, many V1 cells function as local spatio-temporal filters, responsive to oriented bars (Hubel & Wiesel 1968), V2 cells respond to illusory contours of figures (Peterhans & von der Heydt 1991), some V4 cells respond only if a stimulus has a specific color or pattern (Gallant et al. 1993, Schein & Desimone 1990), and in occipito-temporal regions cells respond selectively to particular shapes (Booth & Rolls 1998, Desimone et al. 1984, Fujita et al. 1992, Kobatake & Tanaka 1994, Logothetis et al. 1995, Sigala & Logothetis 2002, Tanaka 1993, Wachsmuth et al. 1994).

We examined hierarchical processing along a sequence of ventral visual areas as a function of three criteria: (a) retinotopy, (b) motion sensitivity, and (c) object selectivity (Figure 9). Early retinotopic areas V1, V2, and V3 show a high degree of retinotopy (large print in Figure 9) but a low degree of specificity to either motion or form. Intermediate visual areas such as V3a and hV4 exhibit a lesser degree of retinotopic specificity (intermediate print) and, to some extent, higher stronger responses to objects (versus textures) and moving (versus stationary) low-contrast gratings. Higher-level areas along the processing stream show coarser retinotopy (small print in Figure 9) and a higher degree of specialization. For example, MT shows a strong preference for moving versus stationary stimuli but does not exhibit object selectivity. In contrast LO responds more strongly to objects compared to scenes and textures but has little response for moving versus stationary gratings.

This analysis demonstrates the ability to quantify and assess with fMRI a processing stream along several dimensions of visual computations. These analyses can be extended easily to incorporate additional attributes of visual processing such as color or stereopsis to reveal the hierarchy of computations and representations relevant to these domains.

Hierarchical Processing Along the Ventral Pathway: Local-Image Processing in Early Retinotopic Areas but Not in LOC

Several studies show that activity in early retinotopic areas is correlated with local, low-level aspects of the stimuli and perception of these low-level features. For example, increasing the level of contrast of a stimulus monotonically increases the strength of the fMRI signal in V1 (Avidan et al. 2002a, Boynton et al. 1999). Importantly, Boynton et al. (1999) found that contrast-response functions in early retinotopic areas were consistent with psychophysically measured contrast increment thresholds, which suggests that these early visual areas are involved in contrast detection. Indeed a more recent study (Ress & Heeger 2003) indicates that the activation in early retinotopic cortex predicts the ability of a subject to detect low-contrast patterns embedded in noise. However, as one proceeds along the sequence of visual areas in the ventral stream, higher-level areas along the hierarchy show a more invariant tuning to contrast. Avidan et al. (2002a) showed

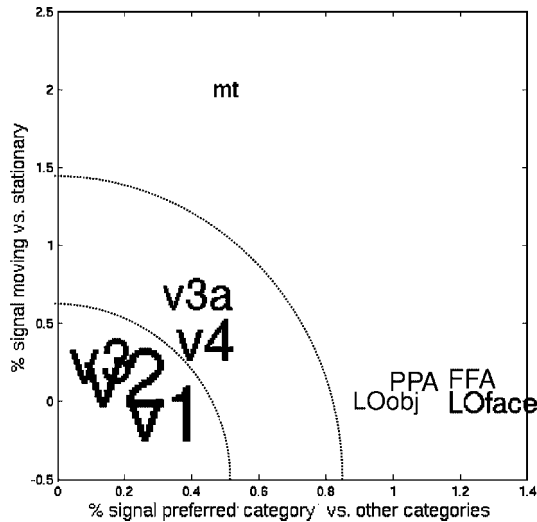


Figure 9 Hierarchical processing in the visual system. Visual areas are plotted as points in a space defined by motion selectivity and category preference averaged across five subjects. The font size illustrates the third dimension of this space: retinotopy (see below). X-axis denotes the object selectivity defined as the average signal (preferred object category) to average signal (nonpreferred categories). Stimuli included unfamiliar objects, faces, and scenes. Y-axis denotes signal (moving low-contrast gratings) to % signal (stationary low-contrast gratings). Retinotopy (denoted by font size) as the difference % signal (preferred eccentricity) to % signal (nonpreferred eccentricity bands) (see Figure 3). In retinotopic areas the measurements were performed on the periphery band. For the FFA and PPA, the measurements were done on the preferred eccentricity band. Dashed arcs indicate putative stages of hierarchical processing.

(Figure 10A) that sensitivity to contrast changes decreases from V1 to LO. Specifically, compared to V1, LO showed a flatter, more invariant contrast tuning curve. V4 showed an intermediate profile, exhibiting less contrast sensitivity than V1 but higher contrast sensitivity than LO (Figure 10A).

Another indication for hierarchical processing comes from measurements of response to object size along the ventral stream (Figure 10B). Again, V1 shows the sharpest sensitivity as peripheral regions in V1 do not respond to intermediate or parafoveal stimuli. V4 shows an intermediate level of tuning, as peripheral regions in V4 do show some response to parafoveal stimuli. Finally, LO shows the flattest (more invariant) curve. Importantly, peripheral regions in LO are significantly activated (but not maximally) by parafoveal stimuli. Recently, several labs have estimated the average receptive field size across retinotopic regions along the ventral and dorsal streams (Kastner et al. 2001, Press et al. 2001, Smith et al. 2001). These studies suggest that the average receptive fields are smallest in V1.

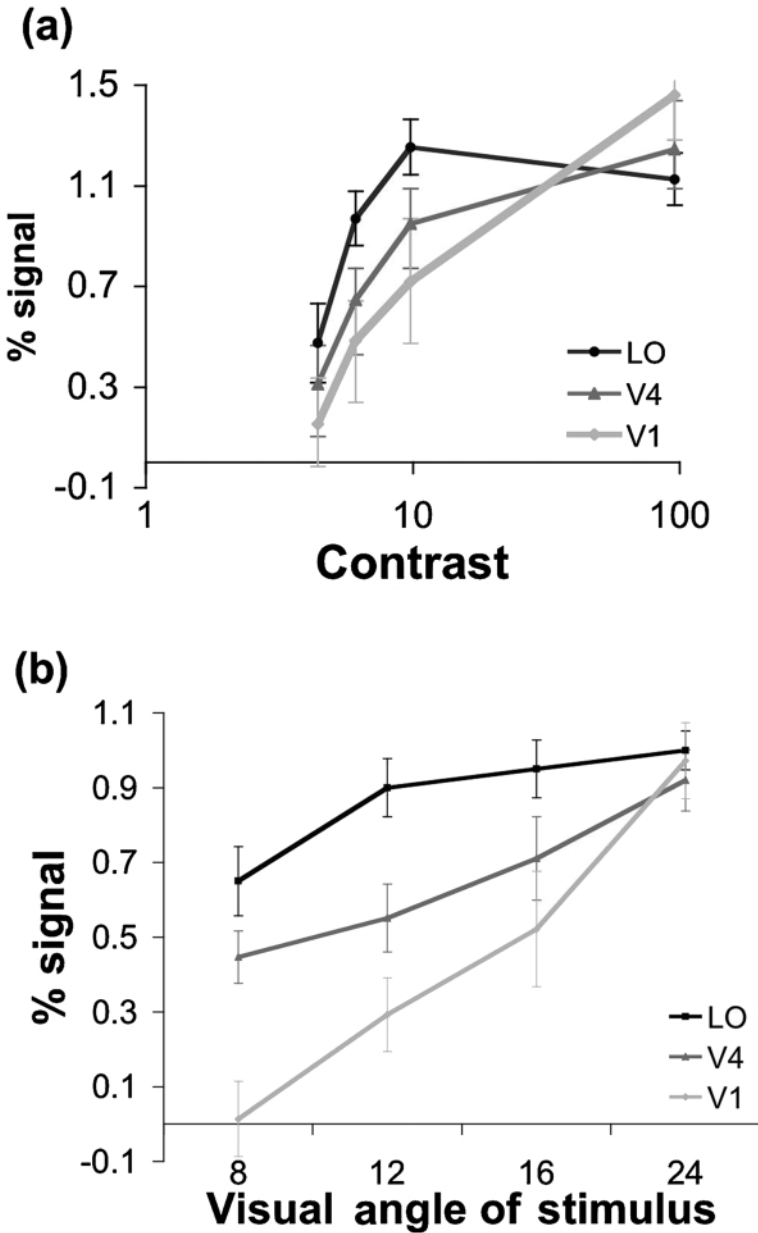


Figure 10 Sensitivity to object contrast and size in retinotopic cortex but not in LOC. (A) Response of visual areas as a function of the contrast of line drawings of face images (Avidan et al. 2002a). (B) Response to object of different sizes measured on the periphery band of several visual areas.

They are larger in V2, larger again in V3/VP, and largest of all in areas V3a and V4.

From Local Low-Level Representations to Abstract Representations

Hierarchical processing is also evident in the transition from the local, low-level functionality of area V1 to the more holistic object responses in LO and VOT (Figure 11A). Gradual scrambling experiments in which object images are broken into an increasingly larger number of fragments reveal areas along the hierarchical sequence that are increasingly more sensitive to image scrambling (Figure 11A) (Grill-Spector et al. 1998b, Lerner et al. 1999). The decrease in activation to scrambled objects in object- and face-selective areas may be related to both receptive field size and stimulus selectivity. Specifically, the object (or face) fragment falling in receptive fields within this area needs to contain a large fraction of the object (or face) to produce activation equivalent to activation levels elicited by whole, unscrambled objects.

The question of how the unified perception of a global shape (or good Gestalt) emerges through hierarchical processing has been addressed recently by Kourtzi and colleagues (Altmann et al. 2003, Kourtzi et al. 2003b). Their experiments measured, using fMRI, the recovery from adaptation to patterns containing randomly oriented lines (Grill-Spector & Malach 2001) after the adapting pattern was changed into a different random pattern or into a pattern containing a colinear contour. They observed that both higher (LO and VOT) and lower visual areas (V1 and V2) were involved in the processing of global shapes, but this processing was related to receptive field size. These results suggest that a global gestalt perception may involve multiple brain areas processing information at several spatial scales.

Additional aspects that emerge as correlated with cortical hierarchy are as follows: (a) susceptibility to repetition-suppression of repeated object images (adaptation) that occurs in higher-level, object-related areas but less so in early retinotopic regions (Avidan et al. 2002b, Grill-Spector & Malach 2001) (the phenomenon of adaptation indicates that responses to objects in object-selective cortex also depends on prior exposure to these stimuli); and (b) increased temporal nonlinearities that suggest increasing levels of persistent activity in high-order visual areas (Ferber et al. 2003, Mukamel et al. 2003). Temporal nonlinearities were also evident in experiments that used a backward masking paradigm in which object and face stimuli were presented briefly and were followed by a noise pattern (Grill-Spector et al. 2000). Activation in V1 did not vary much with stimulus exposure. However, activation in both LO and VOT drastically decreased with shortened exposure durations (Figure 11B). Importantly, the function relating the amplitude of the fMRI signal from LO and VOT was not correlated with exposure duration per se but rather with the psychometric curve of accuracy at an object-recognition task.

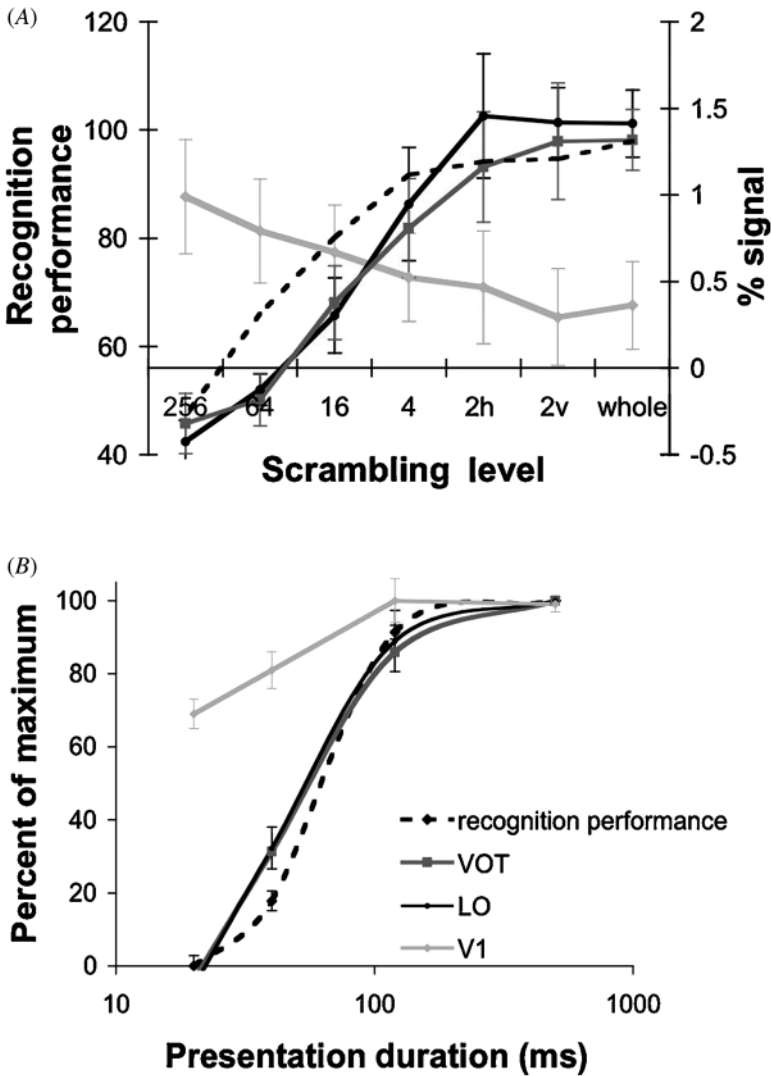


Figure 11 Sensitivity to parameters that affect face and object perception in LO and posterior fusiform (A). Scrambling images into smaller parts reduces the signal in LO and posterior fusiform but not in V1 (Lerner et al. 2001). 2v, scrambling the image into two parts along the vertical axis; 2h, scrambling the image into two parts along the horizontal axis; whole, original, unscrambled face images. (B) Reducing the exposure duration of object and face images reduces the signal in LO and posterior fusiform in a nonlinear fashion that is correlated with subjects' ability to recognize the objects (Grill-Spector et al. 2000).

TOP-DOWN PROCESSING

We focus on many findings concerning feed-forward hierarchical processing. However, both behavioral studies (Driver et al. 2001) and human neuroimaging studies reveal powerful top-down modulations on visual perception and activity patterns in visual cortex (for a review see Kanwisher & Wojciulik 2000). For example, attention and expectation alone without any visual stimulus can produce brain activation in early visual cortex (Chawla et al. 1999, Kastner et al. 1999, Ress et al. 2000). Directing subjects' attention to different locations in the visual field enhances activation in attended locations and inhibits activations in unattended locations (Brefczynski & DeYoe 1999, Macaluso et al. 2000, Tootell & Hadjikhani 2000) with a specificity comparable to retinotopic mapping. Furthermore, attention to different attributes of the visual stimulus, such as color, motion, or form, focally enhances activation in regions involved in processing these attributes. Thus, attending and tracking motion modulates areas engaged in processing motion (Culham et al. 1998, Lavie & Driver 1996, O'Craven et al. 1999), attending to objects and faces enhances activation in object- and face-selective regions, respectively (Avidan et al. 2003, O'Craven et al. 1999, Wojciulik et al. 1998), and attending to color enhances activation along regions involved in color perception (Beauchamp et al. 1999).

These results reveal that in addition to bottom-up processing of the visual stimulus, driven by the input, information feeds back from high-level cortical regions in the parietal and prefrontal cortex to early processing stations. It is still unclear whether the top-down modulations in early visual areas are limited to spatial location, i.e., attentional spotlight, or whether they constitute more complex computations (Galuske et al. 2002, Hochstein & Ahissar 2002, Lamme & Roelfsema 2000, Pascual-Leone & Walsh 2001).

Other top-down mechanisms that may interact and modulate activity in visual areas include spatial coordinate remapping (Merriam et al. 2003), emotional processing (Armony & Dolan 2002, Hendler et al. 2003, Vuilleumier et al. 2002a), and even stereotypical processing (Golby et al. 2001). Top-down effects measured by fMRI are stronger than those reported in single-unit recordings in behaving monkeys. The source of this discrepancy is unclear but may be related to somewhat different aspects of neuronal signals measured by BOLD imaging (Logothetis 2000), compared to single-unit recording employed in physiology.

LARGE-SCALE RELATIONSHIP BETWEEN HIERARCHICAL AND SPECIALIZED PROCESSING

Figure 12 shows a large-scale summary of known visual areas, painted on the unfolded surface of one hemisphere. Close inspection of such an atlas reveals that if the cortex is unfolded by introducing a cut along the calcarine sulcus, thus "opening" area V1 by splitting its horizontal meridian, an intriguing pattern emerges: The two organizing principles, hierarchical processing and functional specialization, are neatly translated into two orthogonal axes laid upon the unfolded human

visual cortex. On the unfolded flat map (Figure 12) the hierarchical progression is arranged along the back-to-front axis (which corresponds to postero-medial to anterior-lateral axis on the real hemisphere), whereas the functional specialization axis is situated orthogonally to the hierarchy axis along the dorso-ventral direction (for axis orientations see hierarchy and specialization labels in Figure 12). Thus, an imaginary line ascending along the hierarchy axis will start from lower area V1 posteriorly and will then ascend in retinotopic cortex going through areas V2, V3, and V3a dorsally and V2, V3, and V4 ventrally, finally reaching into the object-related areas.

Along the axis orthogonal to the hierarchy, i.e. the specialization axis (see label in Figure 12), the visual areas can be examined under the global framework of eccentricity/cortical magnification. Thus, tracing a dorso-ventral imaginary line in early visual cortex (areas V1–V3), eccentricity begins with regions specializing in peripheral vision (peripheral lower-field representation), travels through regions specializing in central vision, at the center of the visual system, and continues ventrally into peripheral representations (this time, upper visual field peripheral representations). A parallel line placed at a higher level of the hierarchy, i.e., more anteriorly along intermediate visual areas (e.g., V3a) will transverse the periphery-center-periphery specialization sequence, but it will now lose the separate upper versus lower visual field representations. Finally, at yet more anterior bands, in high-level, object-selective cortex, one finds a sequence of object-category specializations, which roughly (with some exceptions) parallels the periphery-center-periphery sequence. Regions that respond strongly to places (compared to objects and faces, e.g., the TOS or PPA) are associated with peripheral representations, and regions that respond more strongly to faces (than objects or places, e.g., FFA) are associated with central representations. Thus an imagery line transversing from dorsal to ventral the TOS, LO, FFA, and PPA will encounter the same periphery-center-periphery map revealed in early visual cortex.

To summarize this point, the center/periphery map provides a global organization principle of the entire visual cortex, cutting across the borders between cortical areas. Surprisingly, this center-periphery specialization extends into high-level, occipito-temporal cortex. Here, the center-periphery specialization translates into object-category specialization. Thus, faces (and words) overlap with central representations, and buildings and scenes overlap with peripheral representations (Hasson et al. 2002, 2003a; Levy et al. 2001, Malach et al. 2002). Overall, the two orthogonal axes of hierarchy and center-periphery specialization could provide an overall framework or grid to define, in a fairly orderly manner, the entire constellation of human visual areas.

FUTURE DIRECTIONS

In less than a decade of research, fMRI has provided extensive information and insight about the functional organization of the human visual cortex and correlations between brain activations and visual percepts. However, we only partially

understand how basic visual processes such as color or depth perception are implemented in the human brain, let alone higher-level functions such as object recognition. Further, the relationship between these findings under constrained lab conditions and free viewing in a more natural ecological vision is only beginning to be addressed (Hasson et al. 2004).

Although fMRI is a robust mapping tool and more than a dozen visual areas have been identified, there is consensus about the functional definition of only a handful of visual areas: V1, V2, V3, and probably hMT+. The functional definition of visual areas beyond V3 is currently under vigorous debate. Thus, even the aspect of mapping human visual areas remains a field in which we expect many new findings in the near future. Our recent reports that retinotopic maps extend well beyond “early retinotopic cortex” will be instrumental in delineating high-level visual areas using similar principles, which were applied to early visual cortex.

Another important issue, which is only beginning to be addressed, is long-range developmental and plasticity effects in the human visual system, such as the role of visual experience in instructing the development of cortical circuitry. So far research in this field has focused mainly on pathological conditions (e.g., Amedi et al. 2003, Lerner et al. 2003).

Despite these limitations our ability to investigate the human brain has dramatically increased in the last several years. We are hopeful that the understanding of visual perception and its implementation in the human brain will further increase in the next decade when researchers will successfully combine multiple methods, such as fMRI, DTI, VEP (visual evoked potentials), MEG, psychophysics, and computational modeling, to study the computations involved in visual perception. This explosive growth in our knowledge about the human visual cortex offers the exciting hope that broader issues, such as the relationship between conscious awareness and patterns of brain activation, which have long been central to the human quest for knowledge, finally may be addressed productively.

ACKNOWLEDGMENTS

We thank Galia Avidan, Yulia Lerner, and Uri Hasson for contributing data displayed in the figures. We also thank Rainer Goebel for his help with applications of Brainvoyager relevant to data analysis procedures. Finally, we thank Galia Avidan and Uri Hasson for their comments on drafts of this manuscript.

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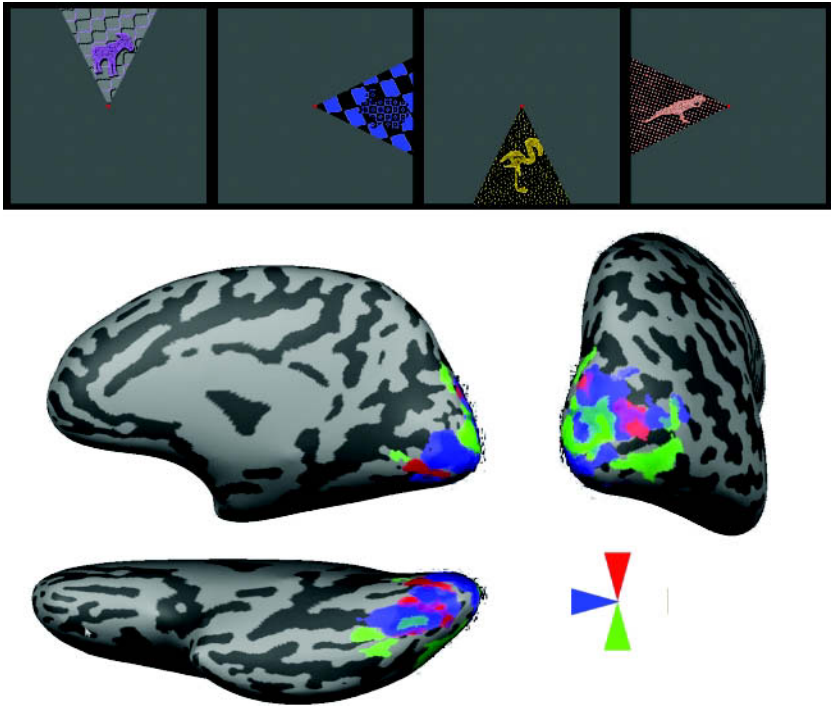


Figure 2 Vertical and horizontal representations in a representative subject. *Top:* Examples of stimuli used in the meridian mapping experiment. Colored objects were displayed on a textured background within each wedge. Stimuli moved back and forth within the wedge during the experiment at a rate of 4 hz. Stimulus radius: 8° *Bottom:* Visual meridians displayed on the inflated right hemisphere of subject EU, displayed from the medial, lateral, and ventral views. Stronger colors indicate higher statistical significance: $10^{-15} < P < 10^{-3}$: Red, blue, and green indicate visual meridians (see icon), purple indicates regions that respond both to the upper and horizontal representations, and turquoise indicates regions that respond both to the horizontal and lower meridian representations.

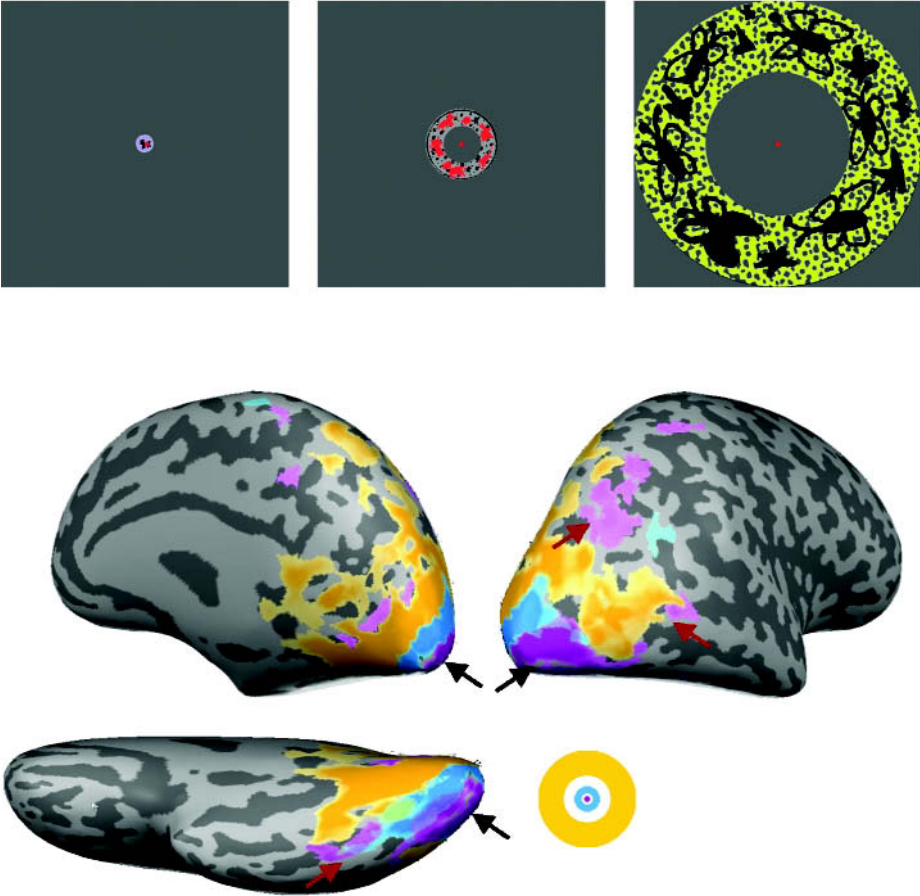


Figure 3 Eccentricity maps in a representative subject. *Top*: Examples of stimuli used in the eccentricity experiment. Stimuli consisted of colored pictures containing objects and textures. Stimuli rotated within the rings at a rate of 2 hz. Stimuli radius: 1.5°, 3–6°, 12–24°. *Bottom*: Eccentricity map of subject EB on the inflated right hemisphere from the medial, lateral, and ventral views. Strong colors indicate high statistical significance, faded colors indicate lower statistical significance: $10^{-15} < P < 10^{-3}$. Pink: central representations (up to 1.5°). Light purple: regions that respond both to central and mid representations. Light blue: parafoveal representations (3–6°). Light green: regions that respond both to mid and peripheral representations. Yellow: peripheral representations: 12–24°. Black arrows indicate the location of the confluent fovea. Red arrows indicate additional fovea in the parietal, lateral temporal, and ventral temporal lobes.

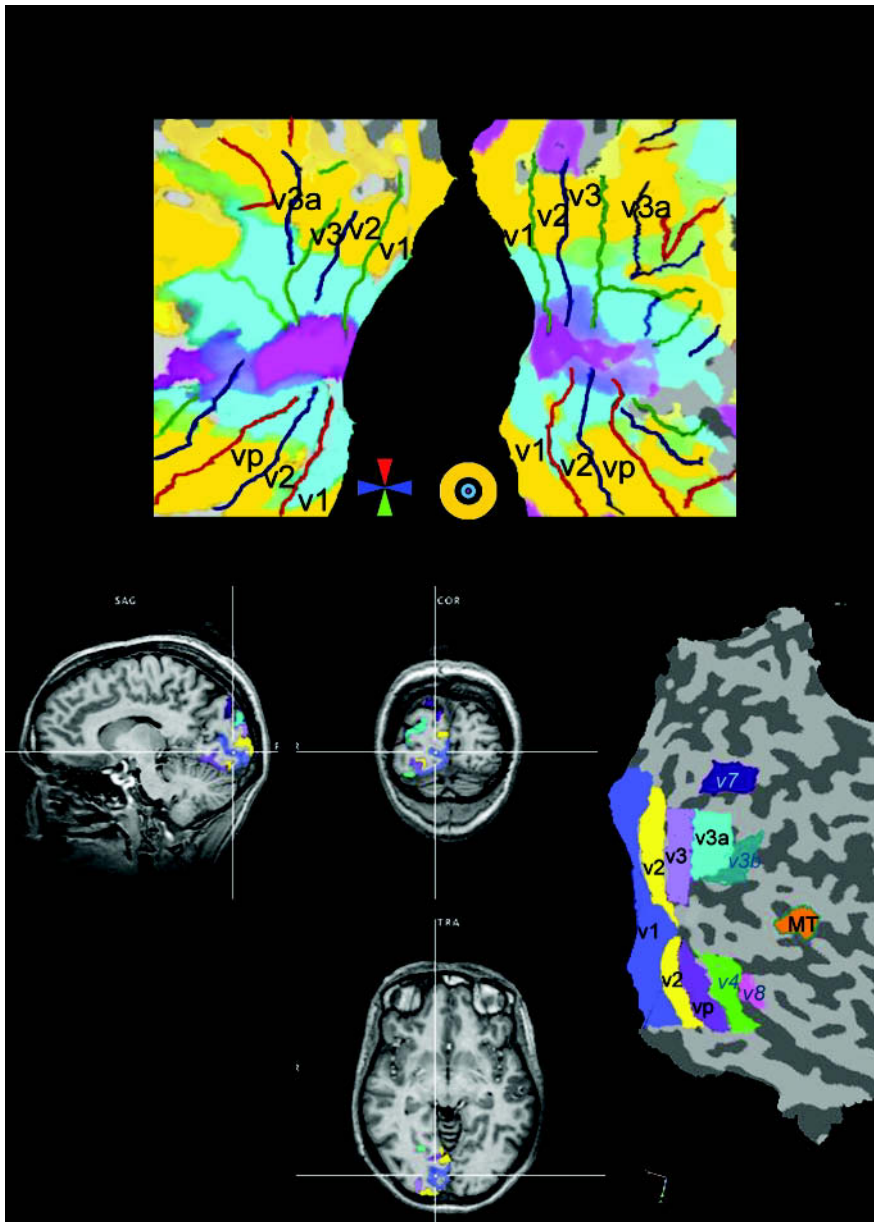


Figure 4 Early and mid-level visual areas. *Top*: Superposition of eccentricity and polar angle maps. Yellow, blue, and pink bands indicate eccentricity maps; lines indicate centers of upper, lower, and horizontal representations (see icons). Note that meridian lines cross all eccentricities orthogonally. *Bottom*: Visual areas on a flattened representation and on the brain volume. Visual area names under consensus are denoted in black, and areas currently under debate are marked in blue italics. All maps in this figure are of subject JHT.

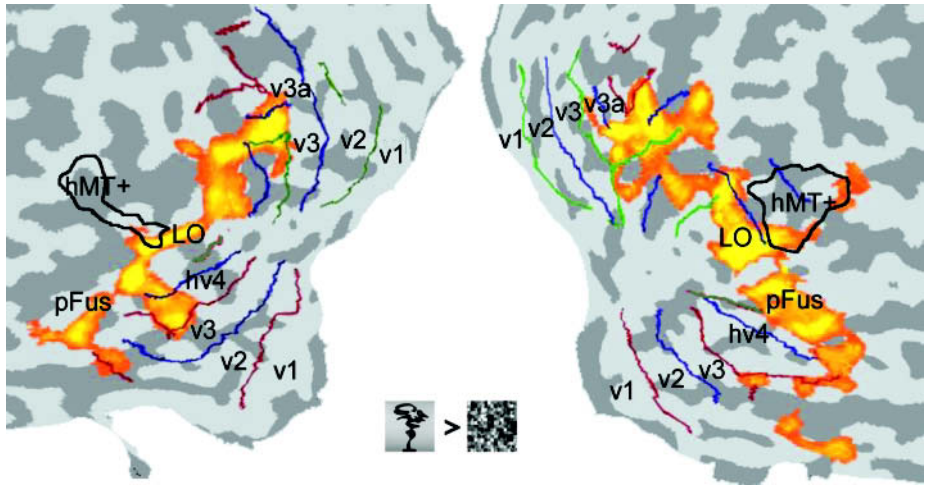


Figure 5 Object-selective regions that respond more strongly to objects than to scrambled objects are displayed on a flattened cortical map (subject EB). Yellow and orange indicate statistical significance: $p < 10^{-12} < p < 10^{-6}$. Colored lines indicate borders of retinotopic visual areas. Area hMT+ was defined as regions in the posterior bank of the inferotemporal sulcus that respond more strongly to moving versus stationary low-contrast gratings (with $p < 10^{-6}$). LO, lateral occipital; pFus, posterior fusiform.

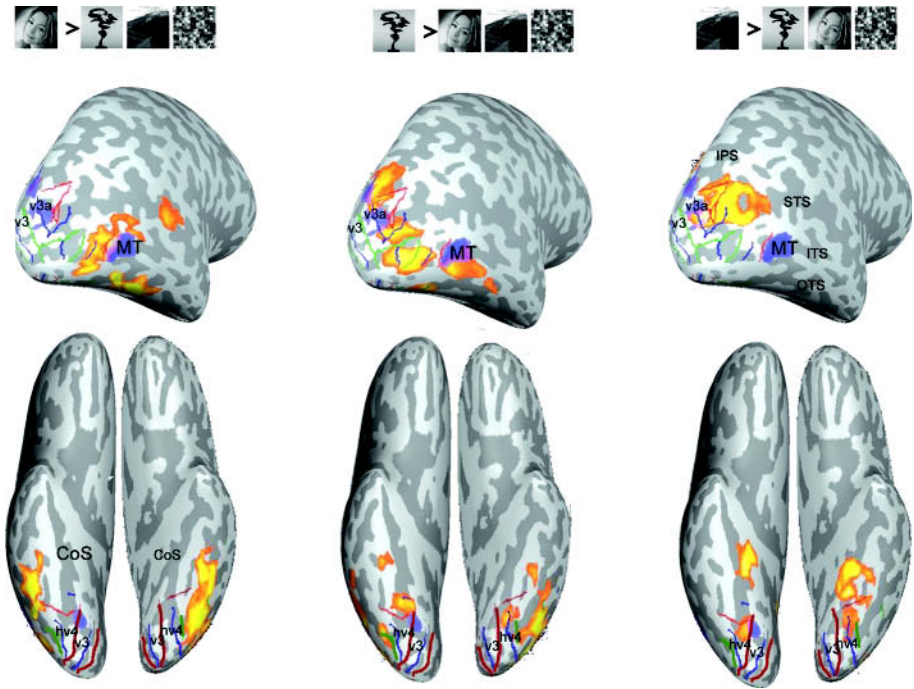


Figure 6 Face-, object-, and place-selective regions in the human brain displayed on an inflated surface representation of subject JHT. Icons indicate the comparison done in the statistical tests. *Left*: areas responding more strongly to faces than objects, places, or textures. *Center*: areas responding more strongly to objects than faces, places, or textures. *Right*: areas responding more strongly to places (scenes) than faces, objects, or textures. Yellow and orange indicate statistical significance: $p < 10^{-12} < p < 10^{-6}$. Colored lines indicate borders of retinotopic visual areas. Blue indicates area hMT+, defined as a region in the posterior bank of the inferotemporal sulcus that responds more strongly to moving versus stationary low-contrast gratings (with $p < 10^{-6}$).

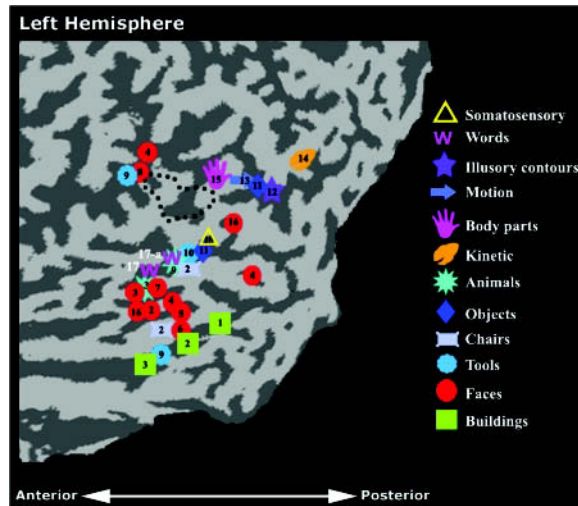
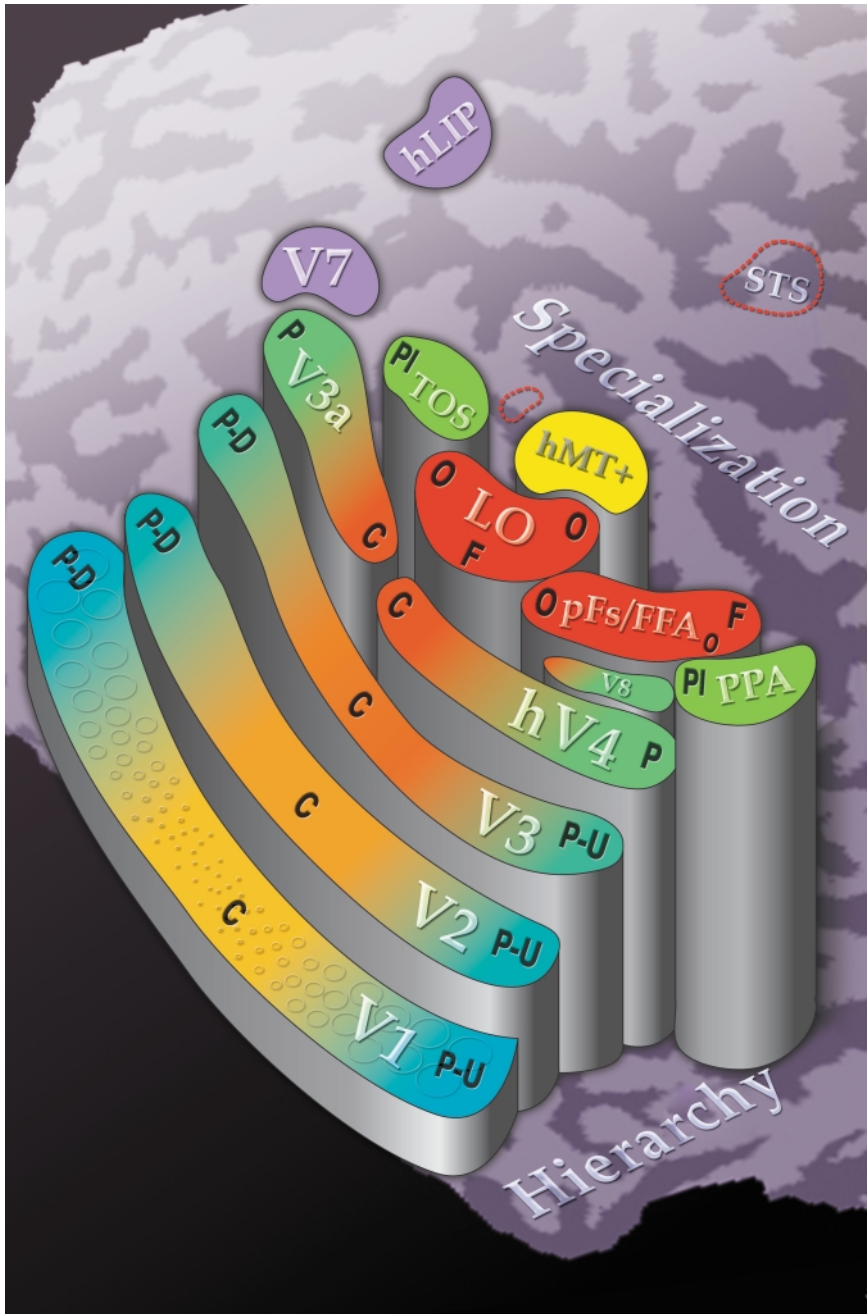


Figure 8 Areas that respond to selected categories: meta-analysis of Talairach coordinates across 18 different studies. Summary of cortical regions showing preferential activations to the following object categories: buildings, faces, tools, chairs, animals, common objects, kinetic movement, body parts, moving objects, illusory contours, words, and haptically defined objects. The numbers appearing on the category icons represent the study number as listed below: **1**, Epstein & Kanwisher 1998; **2**, Ishai et al. 1999; **3**, Maguire et al. 2001; **4**, Hoffman & Haxby 2000; **5**, George et al. 1999; **6**, Kanwisher et al. 1997; **7**, Halgren et al. 1999; **8**, Puce et al. 1998; **9**, Chao et al. 1999; **10**, Beauchamp et al. 2002; **11**, Grill-Spector et al. 1999; **12**, Mendola et al. 1999; **13**, Kourtzi et al. 2001; **14**, Van Oostende et al. 1997; **15**, Downing et al. 2001; **16**, Puce et al. 1996; **17**, Hasson et al. 2003a; **18**, Amedi et al. 2001; **19**, Haxby et al. 1999. The region pertaining to body parts (region 15) is estimated based on the MNI coordinate system. The word-related activation is based on an average activation from six different studies as reported in Hasson et al. 2002. Note the substantial consistency of the various object-related activations across the different studies. Used with permission from Hasson et al. 2003a.



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Figure 12 Schematic atlas of human visual cortex. The schematic layout of human visual areas is presented on an unfolded right hemisphere, illustrating the orthogonal axes of hierarchy and specialization (*labeled along the axis direction*). The visual areas are arranged in a staircase fashion to illustrate the hierarchical sequence of increased abstraction leading from primary visual cortex to high-order visual areas. The orthogonal, specialization axis is illustrated through the color scale. The specialization is manifested in early cortex as a transition from central (*C*) to peripheral (*P*) visual-field representations, associated with high and low magnification factors, respectively. In higher-level cortex, the specialization is manifested as a transition from regions that respond preferentially to objects/faces (*O, F*), and are related to central-biased, high-magnification representations, to regions that respond more strongly to places, buildings, and scenes (*B*) and are related to peripheral-biased, lower-magnification representations. B, buildings/scenes; C, central; P-U, P-D, peripheral representation of upper and lower visual fields, respectively; Pl-, place; F-, faces; O-, objects.