

Occipital Lobe

THE OCCIPITAL LOBE encompasses the posterior portion of the human cerebral cortex and is primarily responsible for vision. The surface area of the human occipital lobe is approximately 12% of the total surface area of the neocortex of the brain. Direct electrical stimulation of the occipital lobe produces visual sensations. Damage to the occipital lobe results in complete or partial blindness or visual agnosia depending on the location and severity of the damage.

Vision begins with the spatial, temporal, and chromatic components of light falling on the photoreceptors of the retina and ends in the perception of the world around us. The occipital lobe contains the bulk of machinery that enables this process. However, our perception of the world is also affected by expectations and attention. Indeed, through extensive feedback to the occipital lobe and other lobes of the brain, especially the parietal and temporal lobes, general cognitive processes influence our visual perception.

VISUAL PATHWAYS: FROM THE RETINA TO THE OCCIPITAL CORTEX

The visual field is directly imaged on the retina by the optics of the eye; hence, the visual field topography translates into retinal topography (retinotopy), which is inverted due to the optical properties of the cornea and lens of the eye. Information from the retina leaves the eye through the optic nerve, which leads to the optical chiasm. Here, the fibers from the nasal side of the fovea in each eye cross over to the opposite side of the brain while the others remain on the same side. The result is that the mapping from external visual fields to the cortex is crossed. Visual information from the left half of the visual field (from both the right and the left eyes) goes to the right half of the brain (right hemisphere), whereas all the information from the right visual field goes to the left hemisphere. The vertical meridian representation of the two hemifields is joined via a large fiber system called the corpus callosum. From the optic chiasm there are two separate pathways that lead to the brain. The smaller one goes to the superior colliculus, a nucleus in the brainstem, which then projects to the thalamic pulvinar nucleus. The larger pathway goes through the lateral geniculate nucleus (LGN) of the

thalamus and to the occipital cortex or primary visual cortex (V1).

MAPPING VISUAL AREAS: RETINOTOPY

Before the functions of the different areas are discussed, we first need to have an accurate map of the visual areas in the occipital lobe. Recently, our understanding of the functional organization of the human brain has greatly expanded due to the development of neuroimaging techniques [mainly functional magnetic resonance imaging (fMRI)] that allow direct noninvasive observation of patterns of brain activity in normal human subjects engaged in sensory, motor, or cognitive tasks. In particular, fMRI has been used to chart the retinotopic and functional organization of the visual cortex in the human brain. Visual field topography has been a primary source of information used to identify and map different visual areas in animals and humans. The mapping from the retina to the primary visual cortex is topographic in that nearby regions on the retina project to nearby regions in V1. In the cortex, neighboring positions in the visual field tend to be represented by groups of neurons that are adjacent to but laterally displaced within the cortical gray matter. This transformation preserves the qualitative spatial relations but distorts quantitative ones. Multiple horizontal and vertical meridian representations are arranged in approximately parallel bands along the cortical surface (Fig. 1, left). These vertical and horizontal meridian representations define the borders between retinotopic regions. Perpendicular to these bands lie isoeccentricity bands (Fig. 1, right);

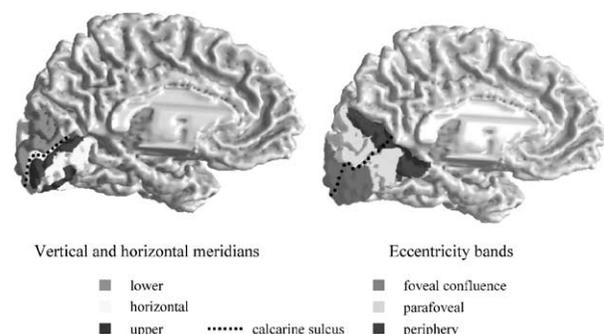


Figure 1

Retinotopic organization of the human visual cortex. Maps of the medial view of the occipital lobe of one subject obtained from fMRI scans performed at the Stanford Imaging Center. (Left) Vertical and horizontal visual meridians. These meridians can be used to define borders between retinotopic areas. (Right) Equal eccentricity bands in the human occipital lobe (courtesy of Brain Wandell and Alyssa Brewer).

however, the representation of the fovea is greatly expanded compared to that of the periphery. In humans, the foveal representation of low-level retinotopic regions converges in the occipital pole and as a person moves anteriorly, bands of mid- and peripheral eccentricity emerge.

In humans, V1 is located in the calcarine sulcus but can extend into the cuneus and lingual gyri (Fig. 2). The representation of the horizontal meridian is contained within the calcarine, such that the upper (dorsal) bank of the calcarine sulcus contains the lower visual field representation and the lower (ventral) bank contains the upper visual field representation. The border between V1 and V2d (dorsal) is marked by a lower field vertical meridian representation, and the border between V1 and V2v (ventral) is marked by an upper field vertical meridian representation. V2d and V2v together provide a second complete representation of the visual field. In the dorsal part of the cuneus, the border between V2d and V3 is marked by another horizontal field representation. In a complementary fashion, in the ventral stream the border between V2v and VP is delineated by another horizontal meridian representation. Both V3 and VP contain a map of a quadrant of the visual field, and combined these areas provide a complete third hemifield representation. In dorsal visual cortex the border between V3 and V3a is marked by a lower visual field representation. V3a

contains a complete hemifield representation, consisting of a lower horizontal and upper visual field representation. Anterior to V3a, an additional hemifield representation is mapped in V7. In ventral cortex the border between VP and V4v is defined by an upper vertical meridian. Researchers are currently debating the functional organization and naming conventions beyond V4v. Some have suggested that V4 consists of a complete hemifield representation comprising an upper horizontal and vertical representation, complementary to the representation in V3a in ventral cortex. Others have suggested an area beyond V4v, termed V8, that consists of an additional hemifield representation.

Beyond retinotopic cortex, the polar angle representation is cruder and the orderly representation of visual meridians is absent. However, the center/periphery organization extends into higher order visual areas. At the junction of the parietal, occipital, and temporal lobes is another visually responsive region that contains a representation that emphasizes the peripheral visual field and is strongly responsive to motion stimuli. This area is termed MT (Fig. 2), and adjacent to it are additional smaller motion responsive areas termed MST (Fig. 2).

Several other visually responsive areas have been identified in the occipital lobe and posterior temporal and parietal lobes, including the kinetic occipital area (KO), which is responsive to motion boundaries, and the lateral occipital complex (LOC), which is selective to objects in the fusiform face area (FFA; which is preferentially activated by faces) and the parahippocampal place area (PPA; which is activated by images of houses and scenes). Since these are higher level areas, the retinotopic representation in these regions is less preserved, and until recently these regions were defined based on their functional selectivity alone. However, the use of more sophisticated methods has revealed that a crude eccentricity organization extends even into higher order areas and correlates to the functional selectivity of these regions.

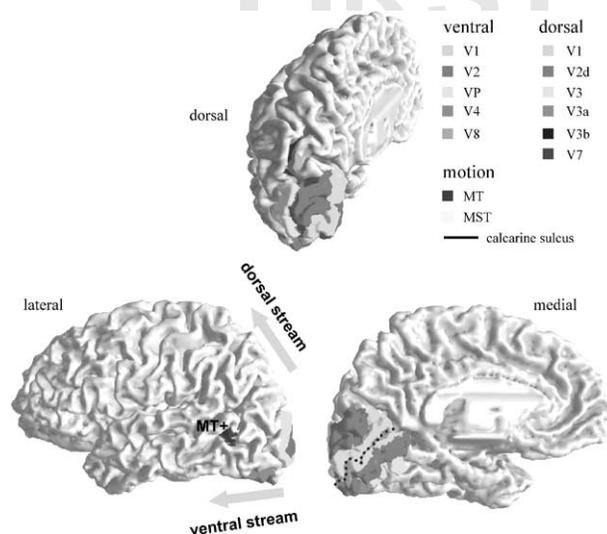


Figure 2

Retinotopic visual areas in the human visual cortex. These maps depict visual areas of a single subject obtained from fMRI scans performed at the Stanford University Imaging Center (courtesy of Brain Wandell and Alyssa Brewer).

“WHAT” AND “WHERE” PROCESSING STREAMS IN THE HUMAN BRAIN

What does each area do? How do these regions subserve our visual perception and cognition? It has been suggested that these multiple visual areas are organized into two hierarchically functionally specialized processing pathways (Fig. 3): an occipito-temporal pathway or ventral stream for object

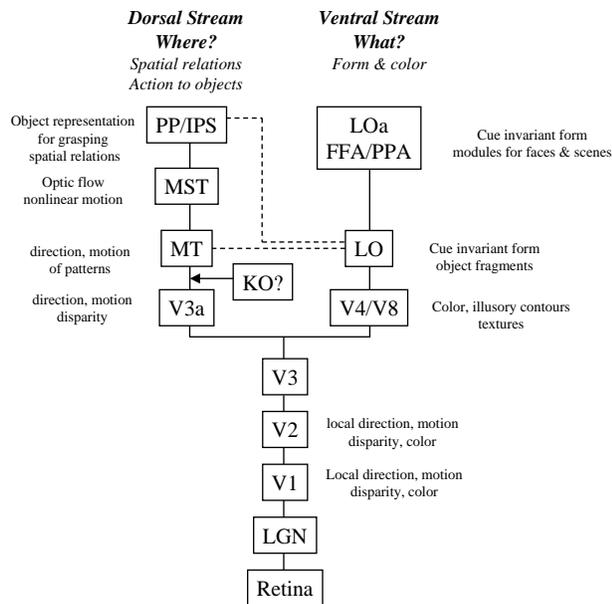


Figure 3
Schematic diagram of “what” and “where” processing streams in human visual cortex. Dashed lines indicate putative connections.

recognition and an occipitoparietal pathway or dorsal stream’ for spatial vision and visually guided actions directed toward objects.

Areas along both the occipitotemporal and occipitoparietal pathways are organized hierarchically, such that low-level inputs are transformed into more useful representations through successive stages of processing. Virtually all visual-processing tasks activate V1 and V2. However, proceeding from one area to the next, the neuronal response properties become increasingly complex. Along the occipitotemporal pathway, for example, many V1 cells function as local spatiotemporal filters, responsive to oriented bars or to particular colors; in V2, cells may respond to illusory contours of figures; in V4, some cells respond only if a stimulus stands out from its background due to a difference in color or form; and in occipitotemporal regions, cells respond selectively to particular shapes. Similarly, proceeding from V1 to MT, new types of directional and motion selectivity emerge. For example, V1 is sensitive to the direction of motion of local components of a complex pattern, whereas MT is sensitive to the global motion of the same pattern.

Thus, much of the neural mechanism for both object vision and spatial vision can be viewed as “bottom-up” processes subserved by feedforward projections between successive pairs of areas within a pathway. However, anatomical studies have shown

that each of these feedforward projections is reciprocated by a feedback projection. Projections from higher order processing stages to lower order ones may mediate “top-down” aspects of visual cognition, such as expectation, context, or attention, that affect our visual perception.

FUNCTIONAL SUBSYSTEMS

A further possible relation between anatomical structure and physiological maps is indicated by the hypothesis 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 brain indicate that this segregation of neural pathways begins in the retina, and different compartments within early visual areas project to different high-level areas. In the following sections, the processing that leads to the perception of motion, depth, color, and form in the human brain is discussed.

Motion

Objects in the world move relative to each other and to the viewer in a nearly ceaseless pattern of change. This activity provides a rich source of information about our environment. 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 the structure of an object determined from its coherent motion. Along the dorsal stream many regions are more active when subjects view moving vs stationary stimuli, including areas MT, MST, V3a, KO, parietal occipital cortex, and even low-level areas such as V1 and V2. Given the range of functions that motion processing subserves, this may not be surprising. Indeed, converging evidence suggests that some aspects of motion processing are localized in dedicated modules in the human brain.

The main motion-selective focus in the human brain is a region called MT+, located at the temporoparietoccipital junction (Fig. 2). Human MT (Fig. 2) is selectively activated by moving vs stationary stimuli and exhibits high-contrast sensitivity. Comparison of coherent and incoherent motion of light points (in which dots move independently) reveals a significant change in activation within MT+ that increases linearly with the coherence of motion but reveals little change in early visual areas, consistent with the idea of local

processing of visual properties in early visual areas and global motion processing in later areas. Recently, several elegant studies have used the perceptual illusion of the motion aftereffect to show that human MT contains direction-selective neural populations. In addition, it has been shown that the activation of this area is enhanced when subjects attend to or track motion. Thus, converging evidence from many labs shows that human MT+ response properties parallel both the response properties of single neurons and perception. This inference is further supported by clinical studies revealing that akinetopsia is associated with lesions in the vicinity of MT+.

In addition to MT+, other cortical sites such as V3a are activated by various types of coherent motion stimuli. Some regions (MST) seem to be correlated with the processing of optical flow information. Another specialized motion-related area, the KO area located posterior to MT, is involved in the processing of kinetic boundaries created by discontinuities in motion direction. KO is activated more strongly by kinetic gratings than by luminance-defined gratings, uniform motion, and transparent motion.

Another intriguing aspect of motion cue is related to the perception of biological motion or the motion of people and animals. Humans can perceive biological motion from impoverished visual displays in which points of light are attached to joints of a person moving in an otherwise dark room. From these sparse displays, people can discriminate the type of motion (running, dancing, etc.) as well as the sex of the mover. An area in a small region on the ventral bank of the occipital extent of the superior temporal sulcus, located lateral and anterior to human MT/MST, is selectively activated during viewing of point-light moving figures but not by the random movement or inverted motion of the same lights that comprised the point-light figures or by other biological motions such as hand, eye, or mouth movement.

Depth

Compared to the work that has been performed on motion and form processing, there are fewer studies concerning the processing of depth, surfaces, and three-dimensional (3D) structure. 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 3D stimuli: V1–V3, VP, V3a, and MT+. Of these, V3a appears to be the region most sensitive to changes in the disparity range, although all regions activated by random dot stereograms show a correlation between the amplitude of the fMRI signal and disparity. In contrast, other high-level areas, such as LOC, respond to random dot stereograms only when these stimuli include object-form, but these regions do not seem to be sensitive to the exact disparity values.

Color

The primate retina contains three classes of cones—the L, M, and S cones—that respond preferentially to long-, middle-, and short-wavelength visible light, respectively. Color appearance results from neural processing of these cone signals within the retina and the brain. Perceptual experiments have identified three types of neural pathways that represent color: a red-green pathway that signals differences between L and M cone responses, a blue-yellow pathway that signals differences between S cone responses and a sum of L and M cone responses, and a luminance pathway that signals a sum of L and M cone responses. Two main hypotheses have been proposed that link neural activity and color. One emphasizes regions in cortex that may play a special role in color perception, and the second emphasizes a stream of color processing stages beginning in the retina and extending into the cortex.

Human neuropsychological studies suggest that damage to a cortical region on the ventral surface of the occipital lobe, in the collateral sulcus, interferes with normal color processing. Recently, researchers used fMRI to measure color-related activity in the human brain. They measured the difference in activity caused by achromatic and colored stimuli. The area showing a significant change of activity was located in the collateral sulcus and is the same area implicated in achromatopsia. However, the retinotopic organization of this region is debated. Although the area associated with color signal tends to correspond with the foveal representation, some researchers refer to the area as V4, whereas others suggest the color-responsive area is beyond V4 and that it should be called V8.

Other results from several laboratories show that opponent color signals can be measured in a sequence of visual areas, including early visual areas. For example, for certain stimuli, the most powerful responses in area V1 are caused by lights that excite

opponent color mechanisms. Measurements with contrast-reversing lights and simple rectangular patterns reveal powerful color opponent signals along the pathway from V1 to V2 and V4/V8. Moreover, moving stimuli, seen only by opponent color mechanisms, evoke powerful activations in motion-selective areas located in the lateral portion of the parietooccipital sulcus. Further research should reveal the processing stages and mechanism underlying color perception.

Form Perception and Object Recognition

The LOC, a cortical region located on the posterior aspect of the fusiform gyrus and extending ventrally and dorsally, responds more strongly when people view pictures of either common objects or unfamiliar textures compared to when they view visual textures without obvious shape interpretations. Moreover, studies using event-related potentials recorded from electrodes placed directly on the cortical surface of patients before surgery found object-specific waveforms that show stronger activation for a variety of objects (e.g., cars, flowers, hands, butterflies, and letters) than for scrambled control stimuli. The location of these sites includes the LOC.

The LOC is largely nonretinotopic and is activated by both the contralateral and ipsilateral visual fields. It contains at least two spatially segregated subdivisions, a dorsal caudal subdivision LO (Fig. 4, lateral view) and a ventral anterior subdivision pFs (Fig. 4, ventral view). The LO is situated posterior to MT in the lateral occipital sulcus and extends into the posterior inferior temporal sulcus. The anterior ventral part of the LOC is located bilaterally in the fusiform gyrus and occipitotemporal sulcus. Each of these subdivisions contains a separate foveal representation. The fovea of LO is connected to the confluence of fovea of early visual areas, whereas the pFs contains a separate foveal representation located on the lateral bank of the collateral sulcus and extending into the fusiform gyrus. In ventral cortex there is a consistent relationship between eccentricity maps and object selectivity. Regions that are selective to faces overlap with the representation of the fovea, whereas regions that are selective to houses overlap a peripheral visual representation located in the collateral sulcus (Fig. 5). These experiments suggest that the entire object-selective region may be organized along an eccentricity axis that could be relevant to the way in which humans perceive different object categories.

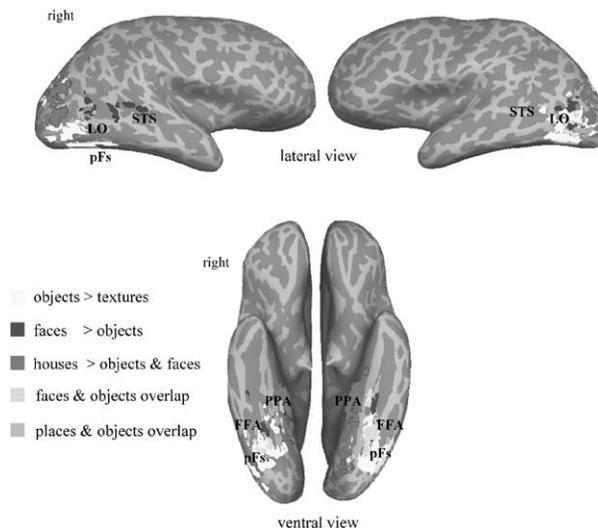


Figure 4
Object-selective regions in the human ventral processing stream. Object-, face-, and place-selective regions are depicted on the inflated brain of one subject. The brain was inflated using specialized software to enable visualization of regions buried inside sulci. Sulci are shaded dark gray and gyri lighter gray. LO, lateral occipital; pFs, posterior fusiform and occipitotemporal sulcus; FFA, fusiform face area; PPA, parahippocampal place area; STS, superior temporal sulcus (experiments were conducted by Kalanit Grill-Spector and Nancy Kanwisher at the MGH imaging center, Charlestown, MA).

Any useful object-recognition system should be relatively insensitive to the precise physical cues that define an object (namely, cue invariance) 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. Indeed, recent studies reveal that the LOC is involved in the representation of shapes rather than the physical properties or local features in the visual stimulus. The LOC responded more strongly when subjects viewed objects defined by either luminance, texture, or motion cues rather than to control stimuli consisting of textures, stationary dot patterns, or coherently moving dots. The same regions were also selectively activated when subjects perceived simple shapes that were created via illusory contours, color contrast, stereo cues, texture boundaries, grayscale photographs of objects, or line drawings. 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.

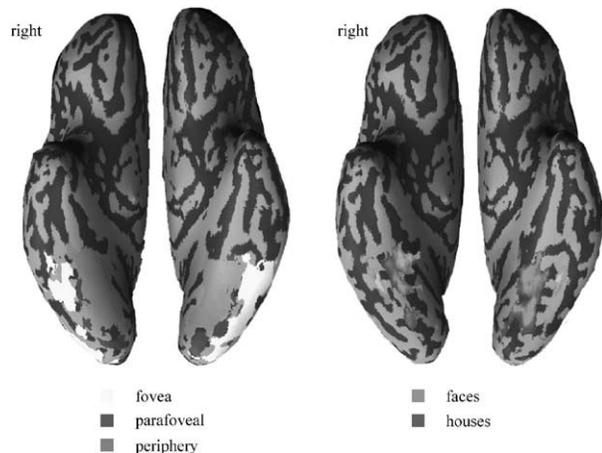


Figure 5

The relation of face and place areas to eccentricity bands. (Left) Eccentricity bands on the ventral view of an inflated brain. (Right) Face and place areas in the same subject. Note that the face area overlaps with foveal representations and the place area overlaps with peripheral representations (maps courtesy of Rafael Malach and Ifat Levy, Weizmann Institute of Science, Israel).

Intriguingly, recent evidence suggests that some regions within the LOC might exhibit not only cue invariance but also modality invariance. In the vicinity of LO, and partially overlapping it, is a region activated more strongly when subjects touch objects but not when they touch textures. Thus, these regions may constitute a neural substrate for the convergence of multimodal object representations.

Although 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. However, evidence from lesion studies demonstrates that damage to the fusiform and occipitotemporal junction results in a variety of recognition deficits. Also, studies in humans have shown that electric stimulation of similar regions interferes with recognition processes or, in some cases, can create an illusory percept of an object or a face. Recent fMRI experiments provide evidence that the activation of ventral occipital cortical regions is correlated to subjects' perception of objects, faces, and houses in a variety of experimental paradigms and tasks. Together, these findings suggest that these regions may be necessary (and perhaps even sufficient) for object recognition.

Within ventral occipitotemporal regions, several areas have been suggested as modules for representing and perceiving specific object categories, such as faces (FFA) and places (PPA) (Fig. 4). One of the most extensively studied areas in recent years is the

FFA. 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, and hands). Other face-selective regions can be found in a more posterior occipital region partially overlapping LO and in a region near the posterior end of the superior temporal sulcus. The PPA, another category-selective region of cortex, responds strongly to a wide variety of stimuli depicting places and/or scenes (e.g., outdoor and indoor scenes and houses) compared to various nonplace control stimuli (e.g., faces or scrambled scenes). The following question arises: How many category-selective regions of cortex exist in the human visual pathway? Selectively activated focal regions of cortex were reported for other categories as well, including animals, tools, letter strings, and even body parts.

Although the basic response properties of the FFA and the PPA are generally agreed upon, what they indicate about the function of these regions is considerably less clear. Some researchers argue that the FFA and the PPA are cortical modules specialized for the recognition of particular object classes that are important in our everyday lives. Thus, the FFA is primarily involved in face recognition and the PPA is involved in scene perception. However, an important unresolved question concerns the functional significance of the responses in these regions to "non-preferred" stimuli, which have less significance than the optimal object class but clearly do have significance. The critical question is whether these lower responses reflect a critical involvement of these stimuli in the representation or recognition of other objects. One possibility is that each object is represented as the entire pattern of activity across all of these regions (LOC, FFA, and PPA), and that it is the distributed representation that forms the basis of object recognition. Another (nonexclusive) possibility, which I favor, is that the FFA, PPA, and LOC are in fact part of the same functional region, which is composed of a set of category-selective and/or feature-selective columns at such a fine scale that they cannot be resolved with fMRI, except for a few very large regions such as the FFA or PPA. Indeed, recent experiments support the idea that the PPA, FFA, and pFs may be part of the same functional area since there is a continuous mapping of eccentricity bands across all these regions. What is the basis of the functional organization in the ventral processing

stream? Is it innate or learned? Is it dependent on the recognition task? Is it based on visual similarity? Future experiments will explore these alternatives.

CONCLUSIONS

Several general organization principles can be extracted from the data summarized in this entry. First, the occipital lobe is composed of a number of distinct visual areas. Second, several of these stages contain a retinotopic representation of the visual field. However, ascending through the processing stages the retinotopic mapping becomes coarser, whereas the functional properties of these areas become more complex. Third, all visual tasks activate an extended network of visual areas, including V1/V2. This is consistent with the idea that processing of visual information requires both local processing in lower visual areas and more complex operations extracting global attributes in high-level stages. Fourth, there is a general tendency of motion and depth processing to activate the dorsal processing stream extending into parietal and mid-temporal cortex, whereas color and form processing tend to activate the ventral processing stream, extending to ventral occipitotemporal areas. Finally, some specific cortical sites are preferentially activated by specific visual attributes (color, V4/V8; motion, MT +) or specific classes of stimuli and tasks (object recognition, LOC; faces, FFA).

Despite the rapid increase of our understanding of human visual areas in recent years, a question that

remains largely unanswered is whether our subjective perceptual visual experience is a consequence of activity in the occipital lobe or whether the occipital lobe only extracts information about the visual world, which is then passed on to other brain areas that mediate awareness. Recent data suggest that there is a correlation between the activity in high-level areas in the occipital lobe and our awareness of the visual world. However, the available evidence is not sufficiently conclusive to determine whether the conscious experience relies exclusively on the occipital lobe or whether the occipital lobe is merely a part of a larger neural circuit that mediates visual awareness.

—Kalanit Grill-Spector

Further Reading

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