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The Brain's Visual World: Representation of Visual Targets in Cerebral Cortex

John H. R. Maunsell

Microelectrode recordings from behaving monkeys have shown that neuronal responses in the visual cerebral cortex can depend greatly on which aspect of the scene is the target of the animal's attention. Accumulating evidence suggests that while the early stages of the visual pathway provide a faithful representation of the retinal image, later stages of processing in the visual cortex hold representations that emphasize the viewer's current interest. By filtering out irrelevant signals and adding information about objects whose presence is remembered or inferred, the cortex creates an edited representation of the visual world that is dynamically modified to suit the immediate goals of the viewer.

Research over the last three decades has yielded a wealth of information about the neural mechanisms underlying vision. Dozens of cortical visual areas have been characterized (Fig. 1), and the visual information encoded by neurons has been shown to differ greatly between areas (*1*). Whereas neurons in the primary visual area V1 (striate cortex) respond well to edges or bars of light, those at later stages of processing represent increasingly complex aspects of the retinal image (*2*). Neurons in later stages of the visual cortex can be extremely selective, responding only to specific, complex forms or patterns of motion (*3*). Thus, vision is supported by levels of cortical processing that collectively cover a range of stimulus attributes, from simple to complex. A widely held view is that the primary reason for these multiple levels is to generate this range of sensory representations.

Creating representations of the retinal image is, however, just one component of vision. Vision is an active process that selects a limited part of the visual image for concentrated attention. Although unselected portions of the image are not lost to perception, at any moment we can give full attention only to a severely limited amount of visual information (*4*). Once this subset of signals has been selected, it must then be interpreted. Thus, the events leading to visual awareness include a substantial editing process that de-emphasizes irrelevant information and adds interpretations and inferences about the meaning of the targeted information.

Studies of macaque monkeys have shown that this editing of visual signals begins in relatively early stages of processing in the cerebral cortex. What the observer is trying to see and what that observer knows about

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the visual scene have considerable impact on what is represented in the visual cortex. These studies show that most areas in the visual cortex, even those at relatively early stages of processing do not give equal weight to all parts of the retinal image. Instead, they preferentially represent those elements to which the observer is paying attention. As more studies have examined the influence of attention on cortical representations, it has come to be seen as an increasingly important factor in determining patterns of activity in the visual cortex.

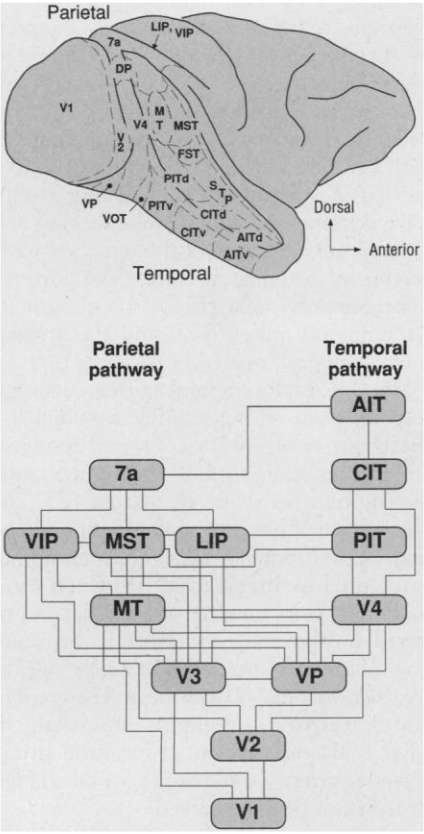

Fig. 1. Visual areas in the cerebral cortex of the macaque monkey. A lateral view of the right cerebral hemisphere is shown, with fine dashed lines marking the approximate location of borders between visual areas. The superior temporal sulcus has been pried open to reveal areas that are normally hidden from view. Additional areas are out of sight in other sulci or on the medial surface. The lower panel shows the hierarchical organization of the better characterized visual areas (*2*). Lines linking the areas represent major axonal projections that have been identified. Earlier stages of processing are at the bottom, and the latest stages are at the top. Areas in the later stages can be assigned to two different streams of processing, the parietal and temporal pathways (*16*). Abbreviations: 7a, Brodmann's area 7a; AIT, anterior inferotemporal area (d, v: dorsal and ventral subdivisions, respectively); CIT, central inferotemporal area (d, v: dorsal and ventral subdivisions); DP, dorsal parietal area; FST, fundus of the superior temporal area; LIP, lateral intraparietal area; MST, medial superior temporal area; MT, middle temporal area; PIT, posterior inferotemporal area (d, v: dorsal and ventral subdivisions); STP, superior temporal polysensory area; V1, visual area 1 (striate cortex); V2, visual area 2; V4, visual area 4; VIP, ventral intraparietal area; VOT, ventral occipitotemporal area; and VP, ventral posterior area.

These findings are changing the way that we view the visual cortex. The established view that cortical areas exist to extract and represent various sensory attributes of the retinal image is clearly missing an essential aspect of cortical representations. The differences between early and later stages of visual processing include not only changes in the complexity of the stimulus attributes that they represent, but also a transition from veridical representations of the visual image to representations that accentuate the viewer's current subject of interest.

Modulation of Neuronal Representations by Behavioral State

While technologies for exploring the functional organization of the human brain have advanced rapidly in recent years, animal models remain the only source of detailed information about how neurons encode visual information. The macaque is an excellent model for the human visual system, possessing visual capabilities that are comparable to those of humans. Microelectrodes can be used to record the action potentials of individual neurons in trained, behaving monkeys. These experiments have shown that the responses of some cortical neurons to a given visual stimulus depend on the behavioral significance of that stimulus (*5*, *6*). Current research is directed at establishing the strength and incidence of these effects in different cortical areas.

To illustrate the effects of attention (*7*) (Fig. 2), we recorded responses from a neuron in area V4 (Fig. 1) while a monkey performed a task in which two stimuli were presented on a screen. One stimulus fell on the receptive field of the neuron; the other did not. On a given trial, the animal was instructed to attend to only one of the two stimuli. The aim was to determine whether attention alone would modify the firing rate of the neuron (*8*). The neuron of Fig. 2, like many in the later stages of the visual cortex, responded more strongly to the receptive field stimulus when the animal paid attention to that stimulus than when the animal paid attention to the other stimulus. The neuron of Fig. 2 responded to the stimulus in its receptive field with about 50% more action potentials when the animal was attending to that stimulus.

An important technical consideration in such experiments is that the retinal stimulation be the same regardless of which stimulus is the target of attention. If stimuli activate different parts of the retina when the animal shifts its attention, then visual neurons might respond differently just because the stimuli are in different retinal locations. For this reason, the animal's eye position is monitored and the animal is trained to attend to a stimulus without looking at it directly, holding its gaze fixed on a small fixation point. By using this approach to ensure that the retinal stimulation is the same, differences in neuronal responsiveness can be attributed to whether the animal is attending to the stimulus in the receptive field.

Many experiments have shown that, as in the example in Fig. 2, the responses of cortical neurons can vary with behavioral state. Because the structures and mechanisms that mediate these response modulations have not been identified, they are simply called "state-dependent modulations" to signify their dependence on behavioral state. State-dependent modulations are a subset of the signals in the visual cortex that arise from sources other than

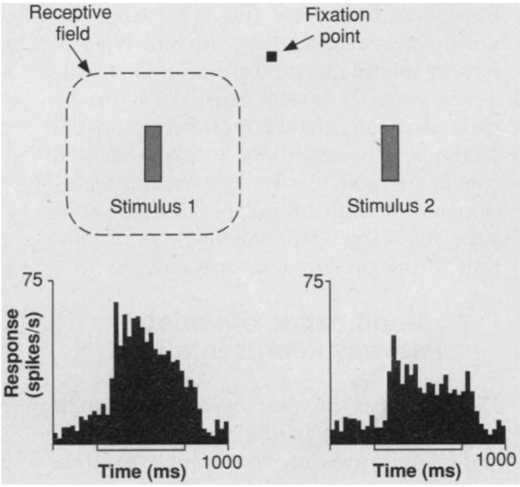

Fig. 2. Behavioral modulation of the responses of a neuron in area V4. The upper panel is a schematic representation of the stimulus configuration. Stimulus 1 was centered in the receptive field of the neuron being recorded. Stimulus 2 was positioned in the other half of the visual field. The animal could be instructed to attend to either one of these stimuli (*8*). The lower panels show the neuron's responses to the receptive field stimulus sorted according to whether the animal was attending to that stimulus (attending to stimulus 1, left; attending to stimulus 2, right). Each histogram shows the rate of firing as a function of time before and during the presentation of the stimuli. A bar below the *x* axis marks the period when both stimuli were present. Each plot is the average of 12 stimulus presentations. The average rate at which this neuron fired spikes was about 50% greater when the animal was attending to the stimulus in its receptive field.

the retina (extraretinal signals). Other types of extraretinal signals are most easily described as sensory or motor signals. For example, neurons in the parietal cortex can be influenced by vestibular signals (*9*), by proprioceptive signals from the neck (*10*), or by the position of the eyes in their orbits (*11–13*). These extraretinal signals are likely to be distinct from those related to behavioral state and may instead help transform retinal locations to body-based or world-based coordinates. They will not be considered here.

Much current work aims to establish the types of state-dependent modulations found in different regions of the visual cortex. One important issue is whether neurons in V1, the earliest stage of visual cortex, are appreciably affected by behavioral state. Unfortunately, this question is difficult to answer. Receptive fields in V1 are tiny and exquisitely sensitive to small displacements of a visual stimulus. Even when eye position is monitored and controlled precisely, it is difficult to guarantee that changes in the response of a V1 neuron between behavioral states do not arise from small, systematic differences in eye position between those states. Problems in providing adequate controls for artifacts of this sort make some reports of state-dependent effects in V1 difficult to interpret. Although there is currently little unequivocal evidence for strong or selective modulation by attention in V1 (*14, 15*), the question of whether substantial state-dependent modulations exist in V1 remains unresolved.

Most studies of state-dependent modulations have examined areas beyond V1 (extrastriate visual cortex). Neurons in extrastriate cortical areas have larger receptive fields, and it is generally easier to demonstrate that visual stimulation is equivalent between behavioral states. In these areas, substantial state-dependent effects have been found. The extrastriate cortex is divided into two streams of sensory processing, parietal and temporal (Fig. 1), each comprising areas representing different types of sensory information and contributing to different visual behaviors (*16*). Areas in the parietal stream analyze motion and spatial relations, whereas those in the temporal stream are more involved in visual recognition and identification (*17*). Here, we consider state-dependent modulations of neurons in the two streams separately.

Modification of Parietal Pathway Representations

Diverse types of state-dependent signals have been found in the parietal pathway, and many of these are consistent with a role in attending to spatial locations or movements. About half of the neurons in and around area 7a show modulation in their responses to a stimulus within their receptive fields, depending on whether the animal is required to attend to that stimulus. This modulation has been demonstrated in a variety of situations that demand attention to a stimulus: when the stimulus is a target for an eye movement (*11, 12, 18, 19*), when it is a target for a hand movement (*20*), or when a change in its brightness must be detected (*20*). The responses of many neurons double when the stimulus is a target of attention.

Enhancement of relevant information is not the only major modification that takes place in the cortex. State-dependent signals can also activate cortical neurons when no stimulus is present, creating representations of stimuli that are not visible. This has been shown most clearly in experiments that require animals to remember visual stimuli for short periods of time. The lateral intraparietal area (LIP) and area 7a in the parietal pathway have neurons that are active when an animal must remember the location of a visual stimulus that fell within its receptive field and that are silent when the animal must remember other locations (*18, 21–23*). This activation is not simply a persisting visual response. As shown by Gnadt and Andersen (*21*) and Duhamel, Colby, and Goldberg (*23*), neurons can become active even if the relevant stimulus was never presented within their receptive field: If an animal moves its eyes so that the receptive field of a parietal neuron covers a location that previously contained a visual target, that neuron can become active. The fraction of neurons showing selective activation in the absence of a visual stimulus varies from about one-fourth to almost all, depending on cortical area and details of the testing conditions. Although the level of activation is typically a small percentage of that resulting from a visible stimulus, these neurons may provide the neural basis for representing the locations of targets that are no longer in view. The activation of these neurons in the absence of a stimulus shows that editing of the cortical representation includes the addition of signals that represent significant stimuli that are not immediately visible.

Neurons in the parietal pathway encode not only the position, but also the motion, of targets that disappear from view. Many parietal neurons are direction-selective, responding strongly when a stimulus moves through the receptive field in a particular direction and poorly if the same stimulus moves across the field in the opposite direction. About half of the neurons in the medial superior temporal area (MST) (Fig. 1) are also active in situations in which an animal can infer that an unseen stimulus is moving behind an occluding object, provided that the inferred motion is in the neuron's preferred direction (*24*). These neurons may contribute to our ability to track target movements through complex environments in which the target is intermittently occluded by other objects.

Modification of Temporal Pathway Representations

Neurons in the temporal pathway appear to be specialized to represent the features of visual objects, such as color, texture, and shape (*16*). Correspondingly, the state-dependent modulations seen in the temporal pathway often depend on attention to a particular stimulus feature. Many studies have documented behavioral effects in area V4 and in later stages of the temporal pathway in inferotemporal cortex [the posterior inferotemporal area (PIT), the central inferotemporal area (CIT), and the anterior inferotemporal area (AIT)] (Fig. 1).

In the inferotemporal cortex, neuronal responses are stronger when a stimulus is the target of attention (*25*), and responses are further enhanced if the animal must discriminate its shape or texture (*25, 26*). Neurons in V4 and the inferotemporal cortex respond more strongly when an animal is required to attend to, or to search for, a particular color or orientation that is preferred by the cell (*15, 27–32*). Typically, one-quarter to one-half of visually responsive neurons in V4 and the inferotemporal cortex respond differently according to what color, orientation, or form the animal is paying attention to, with 1.5-fold changes in response often observed.

The temporal pathway, like the parietal pathway, contains neurons that encode information about remembered visual stimuli. If an animal performs a matching task that requires it to remember the color or shape of a sample stimulus during a short delay period, some neurons in the inferotemporal cortex are selectively activated during the delay when the animal must remember a particular stimulus (*33, 34*). The memory-related activity that has been reported in the temporal lobe during shape or color memory tasks is, however, less common and weaker than that described for remembered locations in the parietal cortex. The number of cells with significant selective activity during memory tasks is usually about 10 to 20%, and some studies have failed to find any appreciable selective activation (*30, 35*). The magnitude of memory-related activation in the inferotemporal cortex is generally modest. Although neurons respond robustly to visual stimuli, the activation that may be attributed to remembering stimuli is often just a few spikes per second (*30*). It has been suggested that the memory-related activity in the inferotemporal

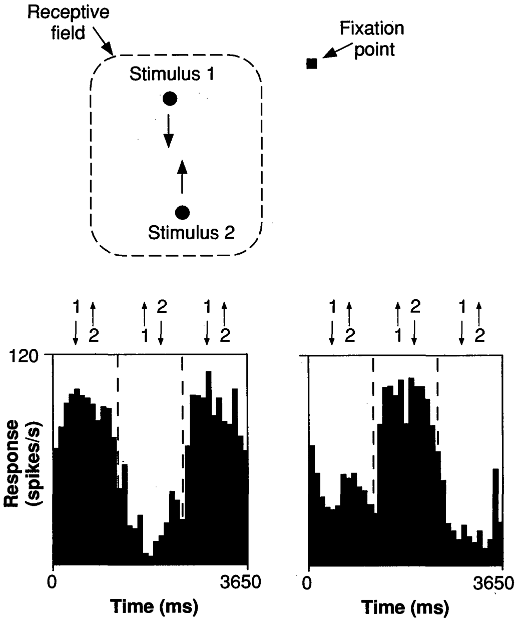

Fig. 3. Modulation of the responses of a neuron in MST. A schematic representation of the stimulus conditions is shown in the upper panel. Two spots of light moved in opposite directions through the receptive field of a neuron that preferred motion in a downward direction. The animal could be instructed to keep track of either one of the spots and to release a lever when that spot changed speed. The lower panels show the responses of the neuron as a function of the spot to which the animal was attending. Each histogram shows two reversals, in which both spots abruptly and simultaneously reversed direction (dashed lines). The motions of the spots are indicated by markers above the histograms. Each histogram is the average of 14 repetitions of one condition. In the left histogram, the animal was attending to stimulus 1, and the neuron responded strongly during the first and third phases, when stimulus 1 was moving downward. In the right histogram, the animal was attending to stimulus 2, and in this case the neuron responded strongly only during the second phase, when that stimulus was moving downward. In both cases, the neuron signaled the motion of the target spot.

cortex may not actually contribute to the process of remembering stimuli because it can sometimes be shut off by the presentation of a distracting stimulus, even when that distracter does not interfere with the animal's memory of the original stimulus (*30, 31, 34*).

The Full Range of State-Dependent Modulations

Are state-dependent modulations as important as sensory signals in determining what is represented in the visual cortex? Although a few studies have described robust state-dependent modulations (*27, 36*), many of the modulations reported are relatively modest (perhaps 25 to 50%). It is likely, however, that the strength of state-dependent modulations is frequently underappreciated. There is little basis for believing that the tests that have been used have revealed the full potential of state-dependent modulations. The difficulty of designing adequate stimuli has long been recognized by investigators studying neurons that prefer complex stimuli. With effort, it is possible to iteratively adjust a stimulus to obtain stronger responses from such neurons (*37*), but because the set of possible stimuli is limitless, investigators must reconcile themselves to the possibility that a neuron might respond more strongly to some untested stimulus. Similarly, at this early stage in our understanding, a failure to find robust state-dependent signals is as likely to reflect an inadequate behavioral task as to be a true feature of the functional organization of visual cortex (*38*).

Indeed, there are hints that the full range of state-dependent modulations is appreciably greater than most studies suggest. Consider, for example, studies that compare neuronal responses when an animal attends to a stimulus in the receptive field with responses when attention is directed to another stimulus. Although the neuronal activity in the latter has been interpreted as an irreducible sensory response, it may actually include substantial state-dependent components. It would be of interest to know what the response to the stimulus would be when no task was performed. Although this comparison has not been made directly, it has been shown that responses to a stimulus that does not require attention are stronger if the stimulus is presented while the animal must hold fixation on a small spot, relative to when the animal performs no task at all (*11, 36, 39*). Mountcastle *et al.* (*36*) found that the responses of 70% of the neurons in area 7a were significantly weaker when the animals were not performing a visual task, with typical reductions being a factor of 3.5. We can predict that state-dependent modulations will be larger and more prevalent than existing studies suggest if neuronal responses when the animal attends to the stimulus are compared with responses when the animal performs no task at all.

Increasing the challenge of the behavioral task may also enhance state-dependent modulations in individual neurons and expand the percentage of neurons that show detectable modulations (*25, 40*). Two recent studies that have used relatively challenging visual displays have found extensive state-dependent effects at intermediate stages of both the parietal and temporal pathways. In one study, Motter (*41*) examined neurons in V4 in the temporal pathway using an array of colored bars rather than just one or two stimuli. When the animal was instructed to attend only to bars of a given color, neurons stimulated by those bars were more responsive and neurons responding to other bars were suppressed. This modulation was reversed midtrial if the animal was given a new instruction that directed it to attend to a different color. About three-quarters of the neurons in V4 had significantly stronger responses when the stimulus in the receptive field was a target, with a twofold enhancement being typical. Other experiments that used a single visual stimulus to examine V4 in behaving monkeys have reported fewer cells with detectable state-dependent modulations (*28*) or modulations that are not as strong (*15, 40*).

Recent experiments in my laboratory (*42*) have demonstrated correspondingly widespread effects in area MST in the parietal pathway. We have found that the responses of almost all neurons in MST are modulated when an animal must keep track of the movements of a single spot that moves among others. The effects are particularly pronounced when the animal pays attention to one of two spots that move simultaneously through a neuron's receptive field. Most neurons in MST are strongly direction-selective. As shown in Fig. 3, when the receptive field of an MST neuron is stimulated by two spots that move in opposite directions, the response of the neuron is largely determined by the direction of motion of the spot to which the animal is attending. The histograms plot responses over a period that included two stimulus reversals, when both spots (stimuli) abruptly reversed direction. When the animal was attending to spot 1 (left), the neuron responded strongly during the phases when spot 1 moved downward, which was the preferred direction for this cell. When the animal was instructed to attend to spot 2, the neuron was responsive only during the other phase, when spot 2 moved downward. Although both spots were always present, the activity of this neuron changed with the animal's attention so as to always signal the direction of motion of the targeted spot. When the animal attended to a third spot that was outside the receptive field, while spots 1 and 2 were stimulating the receptive field, the neuron responded to the two spots with a moderate, steady increase in firing. About 90% of MST neurons showed such changes, with responses usually about twice as strong when the cued spot moved in the preferred direction than when the other spot did.

The widespread state-dependent modulations revealed by these studies show that the overall pattern of activity in V4 and

MST can change markedly depending on what aspect of the visual scene is the focus of attention. It is possible that the prevalence of the effects in these two studies depends on the challenge of a scene that contains multiple stimuli instead of the relatively sparse displays used in most experiments. Although it remains difficult to answer the important question of the quantitative effect of behavioral state on cortical representations, those modulations that have been described can be safely taken as a lower limit to the prevalence and magnitude of state-dependent contributions to cortical activity. There is a real prospect that further studies will show that state-dependent modulations are more extensive than currently envisioned.

Concluding Comments

State-dependent modulations uncouple the representations in the visual cortex from the retinal stimulus. A shift in attention can alter the pattern of activity throughout large regions of visual cortex without any change in the activity in the retina or other early levels in the visual pathway. The existence of state-dependent modulations in later stages of the visual cortex shows that those areas are doing far more than representing complex patterns or forms. By filtering out irrelevant signals and adding information about objects whose presence is remembered or inferred, the cortex creates an edited representation of the visual world that is dynamically modified to suit the immediate goals of the viewer.

The concept that state-dependent modulations play a central role in shaping cortical representations extends our understanding of cortical processing of visual information. Beginning at the level of V1, different classes of sensory signals are directed preferentially into either the parietal or temporal streams of processing (*16*). Each stream contains many hierarchically ordered areas, with early levels representing simple stimulus attributes and later levels representing successively more complex aspects of the visual scene (*2*). In the later stages of both pathways, extraretinal signals such as those arising from vestibular or proprioceptive inputs (not considered here) combine with retinal signals to perform functions such as generating representations in body-centered or world-centered coordinates. Superimposed on this organization is another layer of processing, in which inputs related to behavioral state selectively modulate activity to emphasize those signals that encode information about the viewer's current target.

Although I have focused here on results obtained by recording the responses of individual neurons in monkeys, studies of regional activation in humans have provided consistent, if lower resolution, results (*43*). Nevertheless, a great deal remains to be learned about state-dependent modulations in the cortex. For instance, what is their distribution in the cortex? It is currently unclear whether state-dependent modulations are more pronounced in later stages of the visual cortex or are uniformly strong across all cortical areas. An important short-term goal will be to establish the relative contributions of retinal and state-dependent and other extraretinal inputs at each level of visual processing. Another area of concern is whether any visual areas are devoted exclusively to representing the current target of attention. The activity of some cortical neurons is determined much more by behavioral state than by retinal stimulation, but these neurons are generally intermixed with others that appear to respond to visual stimuli in a more or less mechanical way. Given the difficulty of determining relevant tests for state-dependent inputs, it remains possible that in certain areas virtually all neurons are strongly affected by behavioral state.

A longer-term set of challenges is to decipher the sources of state-dependent inputs to the sensory cortex and the mechanisms by which a behavioral state is generated and maintained. Finally, beyond questions of how and where various types of information are represented lies the imposing problem of how such representations are used to make decisions and to effect behavioral responses. Progress on such questions will be hard-won, but the difficulty of the research is more than balanced by its promise to provide a mechanistic understanding of higher brain function.

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Functional Brain Imaging Studies of Cortical Mechanisms for Memory

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Recent functional brain imaging studies in humans indicate that learning and memory involve many of the same regions of the cortex that process sensory information and control motor output. The forms of perceptual and motor learning that can occur without conscious recollection are mediated in part by contractions and expansions of representations in the sensory and motor cortex. The same regions are also engaged during the conscious storage and retrieval of facts and events, but these types of memory also bring into play structures involved in the active maintenance of memories "on line" and in the establishment of associative links between the information stored in different sensory areas. Although the picture of memory that is emerging from functional imaging studies is consistent with current physiological accounts, there are puzzles and surprises that will be solved only through a combination of human and animal studies.

In the past few years, there has been an explosive growth in the field of human brain imaging (*1*). The goal of some of this work has been to "map" the brain, in the sense of assigning specific functions to structures by selectively activating (or "deactivating") them while people perform various tasks. However, from a neuroscientist's perspective, it is critical not only to ask where changes in activity occur but to understand the underlying mechanisms that produce the changes. To some extent, this question can be approached by new methods of analysis of brain imaging data, such as correlational, time-series, and path analyses (*2*). Probably the most powerful approach, however, is to use brain imaging data to test, where appropriate, specific hypotheses derived from physiological studies in animals, lesion studies in animals and humans, and cognitive theories.

It is important to acknowledge that what we measure in human brain imaging experiments is not neuronal activity but local hemodynamic changes: blood flow, in the case of positron emission tomography (PET) (*3*), and (typically) blood oxygenation, in the case of functional magnetic resonance imaging (fMRI) (*4*). The relation between these hemodynamic changes and the underlying physiology is still inadequately characterized. For simplicity, I will refer to hemodynamic changes as relative "activations" in this review. A further limitation of functional brain imaging is poor temporal and spatial resolution as compared with that obtained with physiological recordings of neuronal activity. Even with fMRI, which provides better resolution than PET, one is still dealing with signals that have latencies of 4 to 8 s and a spatial resolution of about 2 mm, which is a temporal and spatial scale at least one to two orders of magnitude coarser than that of the underlying physiological mechanisms. Nonetheless, functional brain imaging offers a way to study the human brain at work and, it is hoped, to bridge the gap between studies in animals and those in humans.

Because my primary focus will be on memory in the visual modality, I will first review the organization of the visual cortex in monkeys and humans and then examine how knowledge about objects may be stored in this cortex. I will then consider several mechanisms by which experience modifies the way the cortex processes information over both long and short time intervals.

Organization of the Monkey Visual Cortex

The monkey cortex contains at least 30 separate visual areas, occupying about one-half of the total cortex (*5*, *6*). These areas are organized into two functionally specialized processing pathways, each having the primary visual cortex (V1) as its source and each being composed of multiple areas beyond V1 (Fig. 1). The occipitotemporal pathway, or "ventral stream," is crucial for the identification of objects, whereas the occipitoparietal pathway, or "dorsal stream," is crucial for the appreciation of the spatial relations among objects (*7*) as well as the visual guidance of movements toward objects in space (*8*). A simple way to conceptualize the functions of the two streams is "what" versus "where." Both streams have reciprocal connections with systems beyond the modality-specific visual system, including prefrontal areas and the hippocampal region. I will consider the possible role of these connections in a later section.

Why are there so many visual areas, and what does each do? One view is that the pathways are organized hierarchically, in the sense that low-level inputs are transformed into progressively more useful representations through successive stages of processing. Within the ventral stream, for example, the processing of object features begins with simple spatial filtering by cells in V1, but by the time the inferior temporal cortex (area TE; see Fig. 1) is activated, the cells respond selectively to global or overall object features, such as shape, and some cells are even specialized for the analysis of faces (*5*). Likewise, within the dorsal stream, the processing of moving stimuli begins with simple direction-of-motion selectivity by V1 cells, but in the higher-order areas of the parietal cortex (such as LIP and MST; see Fig. 1) the cells respond selectively to complex patterns of motion, such as rotation, and to the optic flow patterns produced when one moves through an environment (*9*).

Organization of the Human Visual Cortex: Processing and Storage

To what extent is the human brain simply a bigger monkey brain, at least as far as the visual cortex is concerned? At the highest

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