

VISUAL PROCESSING IN MONKEY EXTRASTRIATE CORTEX

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INTRODUCTION

The neuronal processes that lead to visual perception have attracted intense interest since Kuffler's studies of receptive field organization in cat retinal ganglion cells over three decades ago (Kuffler 1953). A variety of anatomical and physiological approaches have been employed to analyze the organization of the visual pathway between the retina and striate cortex (V1) and the transformations of visual information that occur at each stage (see Hubel & Wiesel 1977, Stone 1983, Shapley & Lennie 1985). The growth in understanding of the retinostriate pathway has been accompanied by increasing interest in visual processing in the expanse of extrastriate cortex beyond V1. Studies of extrastriate cortex in many species showed that it comprises a mosaic of visual areas that can be distinguished by several anatomical and physiological criteria (reviewed by Kaas 1978, Zeki 1978, Cowey 1979, Van Essen 1979, 1985, Wagor et al 1980, Tusa et al 1981).

The literature in this field is large, and we do not attempt to review all relevant studies. Rather, we concern ourselves with three recent developments that have yielded insight into information processing and flow within extrastriate cortex. The first of these is the convergence of anatom-

ical, physiological, and behavioral results to suggest the existence of distinct streams of processing in extrastriate cortex. This idea has provided a useful conceptual framework for organizing an increasing body of observations and for guiding new experiments. The second development concerns physiological properties that reveal transformations in the information encoded at different stages in visual cortex. Such observations provide clues about the operations performed on the visual image by cortex beyond V1. Experiments with alert, trained animals have led to the third development: the discovery of major and widespread extraretinal influences on neuronal responses even at early stages of the extrastriate pathways. These influences are likely to constitute a major aspect of the neuronal processing in extrastriate cortex and have been neglected in previous studies with anesthetized preparations.

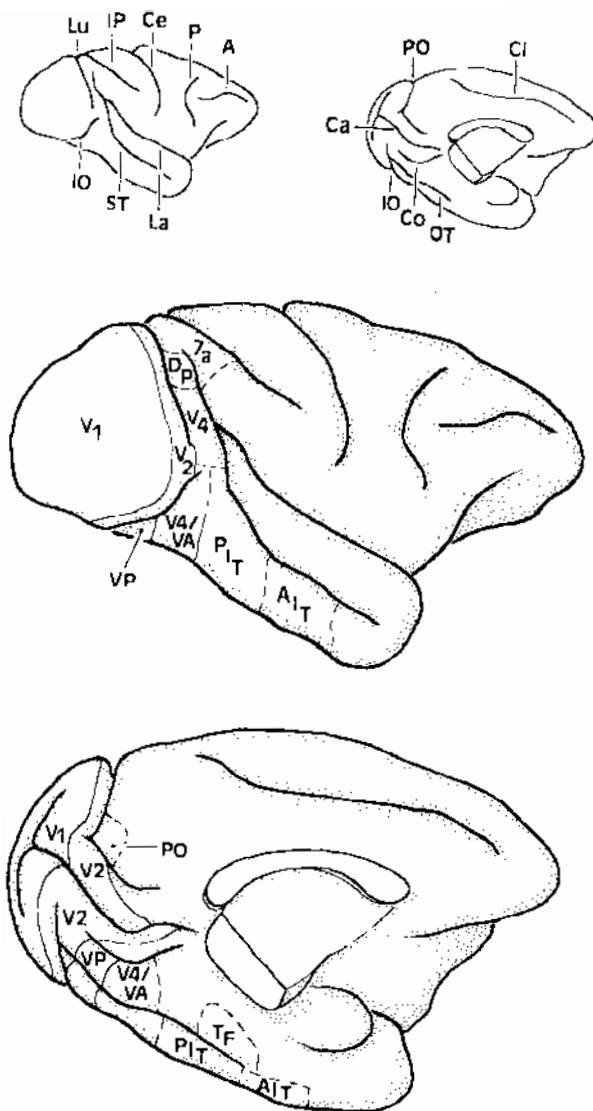
We restrict our discussion to primates because most of the work relevant to these topics has been performed in monkeys. Our discussion focuses on results from the macaque monkey because of the extensive physiological data available for this species. Because of space limitations, we are unable to consider some important topics of active investigation such as stereoscopic mechanisms (reviewed by Poggio & Poggio 1984) and interactions between extrastriate cortex and other brain regions (e.g. Tigges & Tigges 1985).

THE ORGANIZATION OF PRIMATE VISUAL CORTEX

Early evidence that primate extrastriate cortex contains many identifiable visual areas came largely from experiments by Allman & Kaas in the owl monkey and by Zeki in the macaque. In a series of studies Allman & Kaas (1971, 1974a,b, 1975, 1976) showed that owl monkey visual cortex is composed of at least eight visual areas, most of which were found to contain a topographic mapping of the contralateral visual hemifield. In

Figure 1 The location of macaque cortical visual areas. The positions of several visual areas are illustrated on lateral and ventromedial views of the cerebral hemispheres. Outline drawings at the top indicate the major sulci. At least some portion of every visual area is buried within the cortical sulci, and some areas are entirely hidden from view. In this diagram and those that follow, *thin lines* indicate the borders of areas that are reasonably well established, while *dashed lines* mark borders whose position is less well defined. Abbreviations for visual areas: AIT, anterior inferotemporal; DP, dorsal prelunate; PIT, posterior inferotemporal; PO, parieto-occipital; PS, prostriate; VA, ventral anterior; VP, ventral posterior. Abbreviations for sulci: A, arcuate; Ca, calcarine; Ce, central; Ci, cingulate; Co, collateral; IO, inferior occipital; IP, intraparietal; Lu, lunate; La, lateral; OT, occipitotemporal; P, principal; PO, parieto-occipital; ST, superior temporal.

the macaque monkey, Zeki and others demonstrated that visual cortex is subdivided in a related, but not identical manner (Zeki 1969, Cragg 1969, Dubner & Zeki 1971, Zeki 1971, 1975). It is now clear that visually responsive cortex in the macaque occupies a large, contiguous region that includes the entire occipital lobe and large portions of the temporal and



parietal lobes as well (Macko et al 1982). Although some parts of visual cortex remain to be explored, almost 20 areas have already been identified. The location of some of these areas can be seen in Figure 1. The upper of the two drawings is a lateral view of the right cerebral hemisphere, while the lower drawing is a ventromedial view of the left hemisphere. Not all areas are equally well characterized, and for some the exact position or extent of all borders have not been established. *Thin lines* mark the borders of areas that are reasonably well defined, and *dashed lines* mark borders whose position cannot be assigned with confidence.

Macaque neocortex is highly folded, and the major sulci are identified in smaller drawings at the top of the figure. Some portion of each of the visual areas is hidden in one or more sulci, and some visual areas are entirely buried. In Figure 2 the lateral view has been redrawn with selected sulci opened, exposing some visual areas that otherwise are not seen. The upper drawing in Figure 2 shows cortex with the superior temporal sulcus opened, revealing three visual areas that are not visible in Figure 1: the middle temporal area (MT), the medial superior temporal area (MST), and the superior temporal polysensory area (STP). The lower half of Figure 2 shows a hemisphere in which the lunate, inferior occipital, parieto-occipital, and intraparietal sulci have all been opened to varying degrees. In this view it is possible to see parts of V3 and V3A, as well as the portion of the parieto-occipital area (PO) that lies on the medial wall of the intraparietal sulcus.

The shape and surface area of the visual areas can be presented more accurately on an unfolded, two-dimensional map of the cortex (Van Essen & Maunsell 1980), such as that in Figure 3. This map illustrates the entire neocortex from the right hemisphere as though all sulci had been opened and the entire cortex flattened. Visual cortex fills the left side of the map and in the macaque comprises about 60% of neocortex. Although V1 abuts V2 in the intact brain, V1 is shown separated from extrastriate cortex to reduce distortions in the flattened map, as is done in some maps of the earth.

Nineteen areas have been labeled in visual cortex. In sections that follow we discuss the different types of visual information represented in some of these areas. However, it is important to realize that substantial differences exist in the extent of our understanding of individual areas. For example, some areas, such as MT, have been intensively studied using several techniques, while others, such as the ventral intraparietal area (VIP), have been tentatively identified by only one such technique. Future experiments may demonstrate that some currently identified areas are not unitary. For instance, there is accumulating evidence that MST contains two distinct areas (Desimone & Ungerleider 1986, Saito et al 1986).

Van Essen (1985) has recently discussed in detail the extent to which each of these visual areas has been characterized; here we mainly wish to emphasize the types of uncertainty that exist for many areas. Demonstrating that a region of cortex contains a single, identifiable visual area is rarely straightforward. In principle an area can be identified by any of several criteria, including topographic organization, anatomical connections, neuronal response properties, architectonics, and behavioral deficits resulting from ablation. In practice these techniques are often difficult to

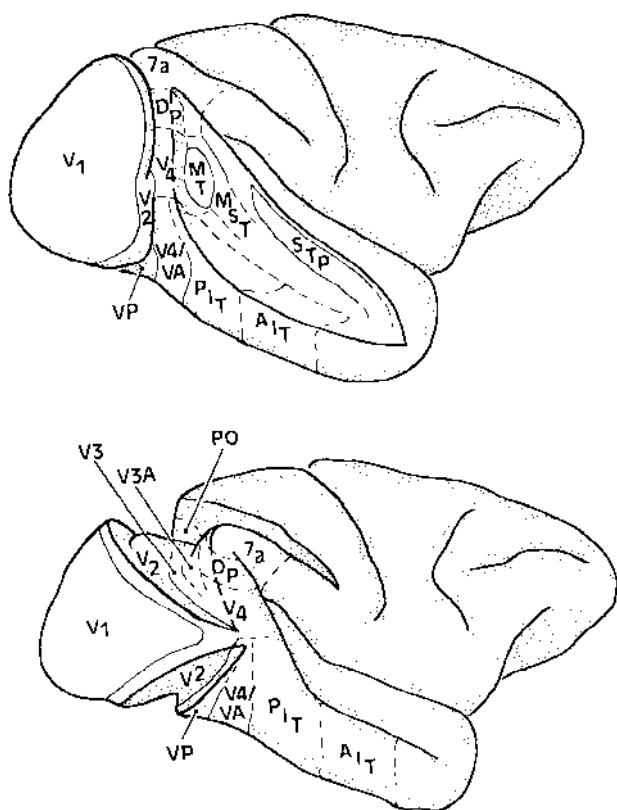


Figure 2 The location of visual areas buried within sulci. The upper half of the figure is a lateral view in which the superior temporal sulcus has been opened to show the positions of visual areas within it. Areas of the superior temporal sulcus that are not visible in the intact view are the middle temporal area (MT), the medial superior temporal area (MST), and the superior temporal polysensory area (STP). The lower half of the figure is a view in which the lunate, intraparietal, parieto-occipital, and inferior occipital sulci have been opened, exposing parts of V3, V3A, and the ventral posterior area (VP). A portion of the parieto-occipital area (PO) can be seen on the medial wall of the intraparietal sulcus.

apply, and their results can be contradictory. For example, V3 and the ventral posterior area (VP) together contain one complete representation of the visual hemifield, but striking differences in their connections, response properties, and architectonics suggest that it may be more appropriate to treat them as different areas (Burkhalter et al 1986). The use of topographic criteria is further complicated in that the representation of the visual field may be either too disorderly to be dependable or simply nonexistent (e.g. Robinson et al 1978, Desimone & Gross 1979), and similar problems occur with other criteria. As a result, identification and localization of specific areas is a complex process and for many areas is not yet complete. The tentative state of our knowledge concerning several visual areas suggests that our subdivision of extrastriate cortex will change with time. However, identification of 19 areas reflects substantial progress in our understanding of the organization of visual cortex beyond V1.

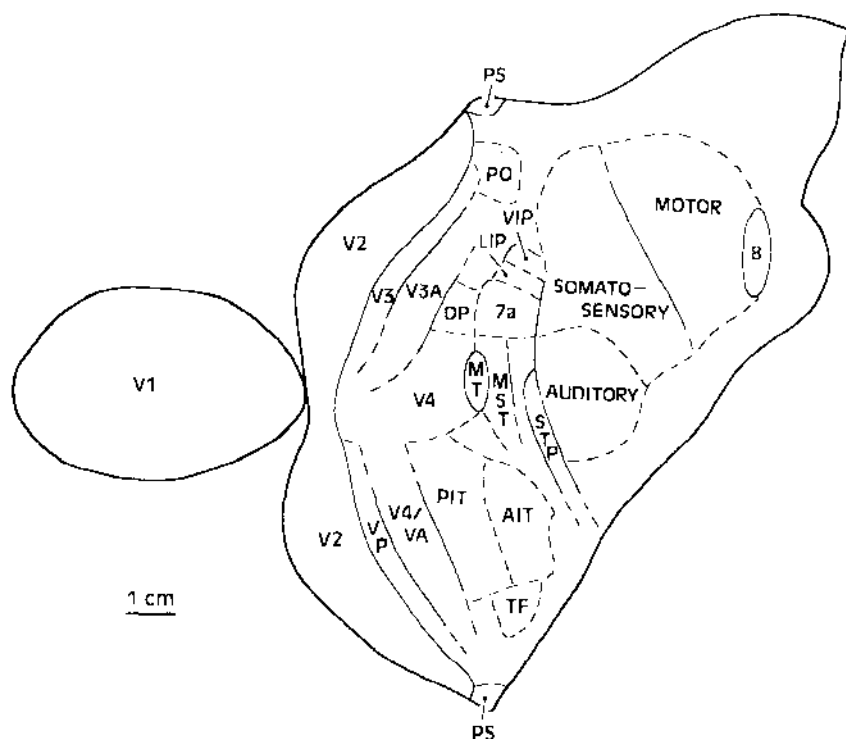


Figure 3 A map of the entire cortex from a right cerebral hemisphere. Visual cortex occupies the left (posterior) side of the map and comprises more than half of cortex. In this flattened representation it is possible to see the relative dimensions of the different cortical areas. Individual areas have not been drawn for other modalities, with the exception of area 8 (the frontal eye fields).

Hierarchical Organization

The identification of this large number of cortical visual areas has led to the discovery of a larger number of connections that transmit information between them. The connections of macaque visual cortex have been recently reviewed by Van Essen (1985), who compiled 84 identified or suspected pathways connecting the 19 visual areas shown in Figure 3. While this number is small compared to the number of possible connections, it is nonetheless sufficient to make the visual cortex a dauntingly complex system to study. Fortunately, macaque visual cortex appears to adhere to organizational principles that simplify its examination. In particular, it is possible to assign cortical areas to different levels of processing based on the laminar distribution of the neurons that connect them.

Several investigators have observed that ascending projections can be distinguished from descending projections by the cortical layers in which they originate and terminate (Jones & Wise 1977, Tigges et al 1977, 1981, Wong-Riley 1978, Rockland & Pandya 1979, Jones et al 1978, Weller & Kaas 1981, Friedman 1983). Ascending projections, which transmit information away from primary sensory areas, arise primarily in the superficial layers of cortex and terminate primarily in layer 4 and the lower part of layer 3. Descending projections, which carry signals back toward primary sensory areas, originate largely from neurons in the deep layers and end primarily in the superficial and deep layers. Most connections among the extrastriate cortical areas have one of these patterns and can be assigned as forward (ascending) or feedback (descending) by these anatomical criteria alone.

These assignments can be used to construct a hierarchy of visual areas by placing each area on a level that puts it above all areas from which it receives a forward projection, and below all those from which it receives a feedback projection (Maunsell & Van Essen 1983c). The hierarchy of macaque cortical areas in Figure 4 does not include some of the areas from Figure 3 because the laminar distributions of their connections are not known. It is important to note that for such a hierarchy to exist, internally consistent rules must be embodied within the total pattern of connections. For example, among reciprocally interconnected pairs of areas there are no cases where both projections are the forward type or both are feedback. It is also necessary that transitivity apply: If area A sends a forward projection to area B, which in turn sends a forward projection to area C, then a projection from A to C must have the forward pattern of laminar termination. All adequately studied connections among visual cortical areas in the macaque conform to this scheme. Although a hierarchical

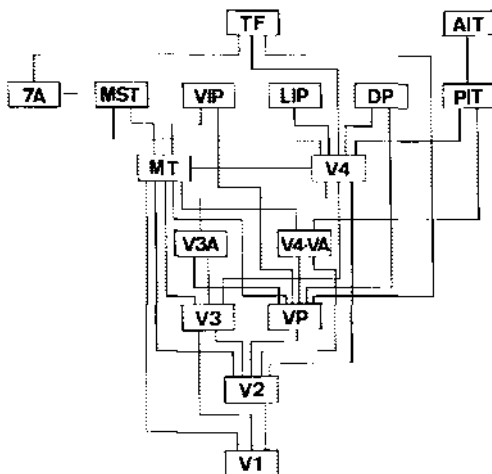


Figure 4 Hierarchy of macaque cortical visual areas. Areas have been assigned to different levels based on anatomical criteria by which connections can be assigned as being forward or feedback. Each area is one level above the highest level from which it receives forward input, and below all levels from which it receives feedback. Concomitantly, each area is above all areas to which it sends a feedback projection, and below those to which it sends a forward projection. The hierarchy is based on connections from numerous studies that were tabulated by Van Essen (1985) and includes only major connections. For clarity, the connections that have been demonstrated in one direction only are not distinguished from others. The connections that exist between V4 and MT do not fit either the forward or feedback category, and have been assigned as "lateral," leaving these two areas on the same level (see Maunsell & Van Essen 1983c).

organization of this nature may not be general for cortex of all mammalian species (see Symonds & Rosenquist 1984), it provides a valuable simplifying framework for considering the flow of information within primate extrastriate cortex.

Two Streams of Processing

Extrastriate areas differ in the types of visual information that they process. The initial evidence for selective processing of visual information in primate extrastriate cortex was obtained in the macaque by Zeki and his collaborators. Dubner & Zeki (1971) found that a region of V1-recipient cortex in the superior temporal sulcus contained a preponderance of neurons that were highly selective for the direction of stimulus motion yet relatively unselective for stimulus color or form (Dubner & Zeki 1971, Zeki 1974b). We refer to this area as MT, the middle temporal visual area, because it is homologous with MT in the owl monkey (Allman & Kaas 1971; see Baker et al 1981, Maunsell & Van Essen 1983a, Albright 1984),

but it has also been called the motion area of the superior temporal sulcus (Zeki 1974b) and V5 (Zeki 1983c). In other studies, Zeki (1973, 1977) identified another area, V4, which was described as containing many neurons selective for color or orientation but few selective for direction of motion. These studies formed the basis for a proposal that each extrastriate visual area was responsible for processing a different type of visual information, such as motion or color (Zeki 1975, 1978).

Recent studies in several laboratories have confirmed early findings of substantial differences in physiological properties between certain visual areas, although the segregation frequently is not as complete as originally envisioned (e.g. Poggio & Fischer 1977, Petersen et al 1980, Schein et al 1982). At the same time, however, some visual areas do process very similar types of visual information (see below). These two observations have been integrated in a notion of functional streams of processing in visual cortex. In this view, visual cortex contains parallel streams of processing that analyze different types of visual information. Each stream involves several areas, with each area representing a different level of processing for a particular type of information.

The idea that primate visual cortex contains distinct streams of processing was formulated by Ungerleider & Mishkin (1982), who described two streams that diverge in the early levels of extrastriate cortex, one leading to visual cortex of the parietal lobe and the other to visual cortex of the temporal lobe. They suggested that these streams are associated with different visual capabilities—the parietal stream is involved in visual assessment of spatial relationships, and the temporal stream is concerned with visual recognition of objects. Support for this hypothesis comes from several lines of research, including anatomical, physiological, and behavioral experiments. In humans, clinical observations indicate that damage to the parietal cortex can affect visual perception of position or movement, yet leave object recognition unimpaired (Ratcliff & Davies-Jones 1972, Damasio & Benton 1979, Zihl et al 1983). In contrast, temporal lobe lesions can produce specific deficits related to object recognition, such as an inability to recognize faces (Meadows 1974a,b, Pearlman et al 1979, Damasio et al 1982, Joynt et al 1985). A corresponding separation of visual functions between the temporal and parietal cortices exists in the macaque monkey. Many studies have shown that lesions of temporal cortex impair visual discrimination of objects, whether the discriminanda differ in color, orientation, brightness, pattern, or shape (see Gross 1973a,b, Dean 1976, 1982, Wilson 1978, Gross et al 1981, Ungerleider & Mishkin 1982, Mishkin et al 1983). Lesions of the parietal cortex, however, leave object discrimination capacities largely intact and instead specifically affect the ability to do tasks related to visual assessment of the location of objects,

such as the visual guidance of hand movements (Pohl 1973, Buchbinder et al 1980, Ungerleider & Mishkin 1982, Weiskrantz & Saunders 1984). Because the parietal and temporal cortices receive inputs from different parts of extrastriate cortex, Ungerleider & Mishkin suggested that these differences in lesion effects reflect the fact that parietal and temporal regions are associated with cortical pathways that process different classes of visual information (see Mishkin et al 1983).

Anatomical and physiological studies now indicate that functional streams of processing exist even at the earliest levels of visual cortex. These streams are present within distinct subdivisions of V1 and V2 and are largely segregated into separate sets of visual areas in later stages of extrastriate cortex. In this review we emphasize two streams for which current evidence is most compelling. One of these streams contains a high proportion of neurons that are selective for properties related to motion, such as direction and speed. The other exhibits more selectivity for color and orientation. We use the terms *motion pathway* and *color and form pathway* (Van Essen & Maunsell 1983) to describe these streams of processing. While these labels are useful for the purposes of discussion, they are unlikely to be completely descriptive. For example, the motion pathway may not be strictly limited to analyzing motion and may not incorporate every aspect of motion. These streams of processing are related to, but are probably not identical with, those described by Ungerleider & Mishkin (1982). The motion pathway appears to contribute visual inputs to parietal cortex, though the relevant connections are not yet fully established. Similarly, the color and form pathway provides inputs to the temporal cortex. However, the motion pathway and the color and form pathways as currently defined probably represent subsets of the information that reaches parietal or temporal cortex and are unlikely to mediate all visual behaviors associated with these brain regions.

Figure 5 shows the areas that we include in the motion and the color and form pathways and their relationships. The motion pathway begins in layer 4b in V1, which contains a high proportion of direction-selective neurons and little or no color sensitivity (Dow 1974, Blasdel & Fitzpatrick 1984, Livingstone & Hubel 1984, Movshon & Newsome 1984, Michael 1985). This layer gives rise to most of the direct projection from V1 to MT. The color and form pathway is found in the superficial layers of V1. These layers contain an array of dot-like patches of cytochrome oxidase rich tissue that have come to be called "blobs" (Horton & Hubel 1980, Humphrey & Hendrickson 1980). Livingstone & Hubel (1984) found that the blobs contain a higher proportion of neurons with color selectivity than the interblob regions. Orientation selectivity, which is taken to convey information about form, was far more common in the interblob regions.

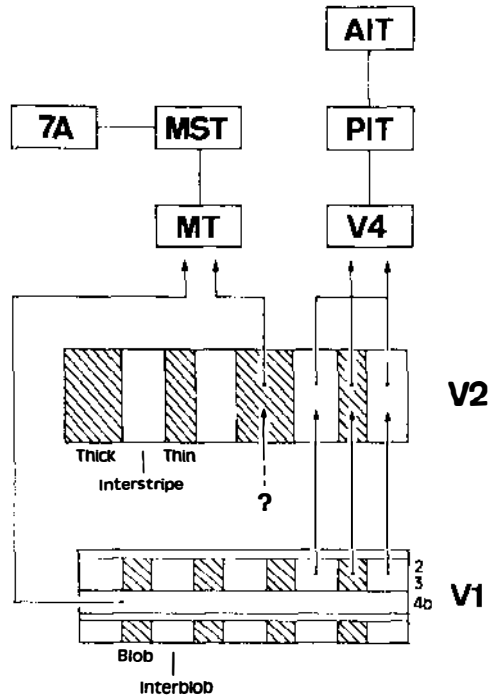


Figure 5 Major components of the motion pathway and the color and form pathway. Segregation of the two pathways is evident in V1, where the color and form pathway arises from the blobs and inter-blob regions in layers 2 and 3. These regions project to the thin stripes and interstripes in V2, which in turn project to V4. The outputs of V4 lead to PIT and AIT. The motion pathway is found in layer 4b in V1, which projects directly to MT. MT also receives a projection from the thick stripes in V2, whose inputs are not yet established. The outputs of MT lead to areas including MST and area 7a.

They suggested that the blob/interblob segregation may represent separate streams for processing color and form information.

Corresponding subdivisions associated with each stream can be found in V2 as well. V2 has regions of high and low cytochrome oxidase activity that are arranged in alternating thin and thick stripes of cytochrome oxidase rich tissue and are separated by interstripe regions with little activity (Tootell et al 1983). The thin stripes receive input from V1 cytochrome oxidase blobs, while the V1 interblob regions project to the V2 interstripe regions (Livingstone & Hubel 1984). Mirroring the functional segregation observed in V1, the V2 thin stripes are enriched in color selectivity while the V2 interstripes contain a relatively high proportion of orientation selective neurons (Hubel & Livingstone 1985). However, both

the thin stripes and interstripes project to V4 (DeYoe & Van Essen 1985, Shipp & Zeki 1985), and we therefore include them both in a single color and form pathway, although it is possible that parallel subdivisions of this pathway persist. The V2 thick stripes project to MT and contain a relatively high proportion of direction-selective neurons (DeYoe & Van Essen 1985, Shipp & Zeki 1985). Whether a projection exists from V1 to the thick stripes remains unknown.

As mentioned above, MT and V4 contain neurons with significantly different response properties. MT neurons are selective not only for the direction of stimulus motion but also for speed and binocular disparity (Zeki 1974a,b, Baker et al 1981, Maunsell & Van Essen 1983a,b, Albright 1984, Felleman & Kaas 1984), thus suggesting that MT is well suited to the analysis of visual motion in three dimensional space. In contrast, V4 contains many neurons that are selective for stimulus color or orientation (Zeki 1978, Desimone et al 1985). The major outputs of MT appear to be relayed to the parietal cortex via intermediate areas, including MST (Jones & Powell 1970, Leichnetz 1980, Mesulam et al 1977). V4 sends a major projection to PIT, the posterior inferotemporal area (Rockland & Pandya 1979, Desimone et al 1980), which in turn projects to AIT, the anterior inferotemporal area (Iwai 1981, Jones & Powell 1970). A separation of motion and color information is also consistent with psychophysical observations that stimuli consisting of only isoluminant colors cannot generate a strong sensation of motion (Ramachandran & Gregory 1978, Cavanagh et al 1984).

It is possible that these pathways originate at earlier stages than V1. The retinostriate pathway contains two markedly different streams that are segregated into the parvocellular and magnocellular subdivisions of the lateral geniculate nucleus (see Stone 1983, Derrington & Lennie 1984, Derrington et al 1984). These subdivisions project to different sublaminae in V1, with layer 4 α receiving magnocellular input and layer 4c β receiving parvocellular input (Hubel & Wiesel 1972). Some evidence suggests that the motion and the color and form pathways arise more or less directly from these subcortical streams (see Maunsell 1986). For example, layer 4 α is strongly connected with layer 4b (Lund & Boothe 1975, Fitzpatrick et al 1985), which projects directly to MT. Similarities between some response properties of neurons in the motion pathway and those in the magnocellular layers of the lateral geniculate nucleus have been noted (Motter & Mountcastle 1981, Maunsell & Van Essen 1983a). In contrast, layer 4c β , which receives parvocellular input, has stronger connections with superficial layers (Fitzpatrick et al 1985), which give rise to the color and form pathway. It is thus possible that the primate visual system contains two subsystems that operate largely in parallel from early sub-

cortical stages to the highest levels of processing in the visual cortex. This striking possibility might be tested by examining responses in the motion or color and form pathway while blocking transmission through one subdivision of the lateral geniculate nucleus.

Although evidence from several different approaches suggests that separate streams of processing exist for motion and for color and form, it seems unlikely that these streams are completely independent. The separation of physiological response properties between the streams, while pronounced, is not complete. For example, direction-selective cells are found in the color and form pathway (Zeki 1978, DeYoe & Van Essen 1985), and neurons in the motion pathway are not devoid of orientation selectivity (Albright 1984). Neither is the anatomical segregation complete, since some connections exist between MT and V4 (Rockland & Pandya 1979, Maunsell & Van Essen 1983c, Ungerleider & Desimone 1986) and between parietal and temporal cortex (Desimone et al 1980, Seltzer & Pandya 1984). In addition, psychophysical (Mayhew & Anstis 1972) and behavioral (Iwai 1985) studies also suggest that some functional overlap exists between the two streams.

While the separation between these streams is not absolute, the evidence discussed above strongly suggests that distinct pathways play a prominent role in processing different types of visual information. Consideration of how physiological properties differ between areas within these pathways adds further support for this scheme of organization. In the sections that follow we consider in detail the transformations of visual signals that occur in these pathways, concerning ourselves first with motion and then with color and form.

THE MOTION PATHWAY

The transformations of the visual image that occur along the motion pathway do not appear to result in increased selectivity for basic parameters such as direction or speed. To the contrary, a recent quantitative study by Albright (1984) has shown that direction tuning in MT is somewhat broader than that in V1. Similarly, retinotopic specificity decreases progressively in successive levels of the pathway. The average receptive field area in MT is 100 times that in V1 (Gattass & Gross 1981), and this trend continues in MST, where receptive fields covering a full quadrant of the visual field can be found (Van Essen et al 1981, Tanaka et al 1986, Desimone & Ungerleider 1986). Rather than sharpening basic tuning curves, the transformation of information between areas in the motion pathway appears to elaborate new, more complex response properties. In the next sections we consider several transformations that occur on the

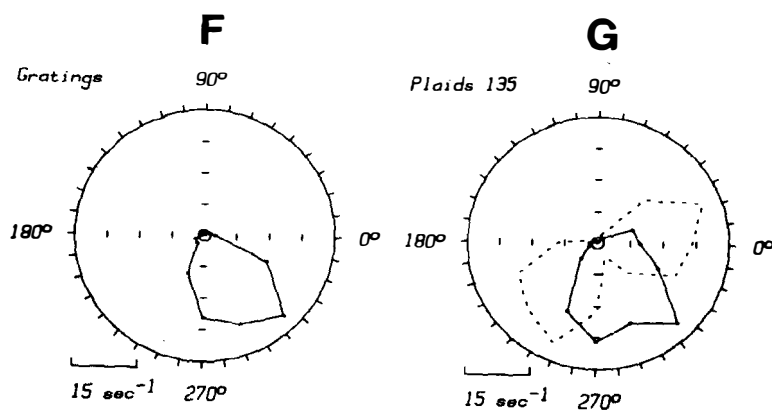
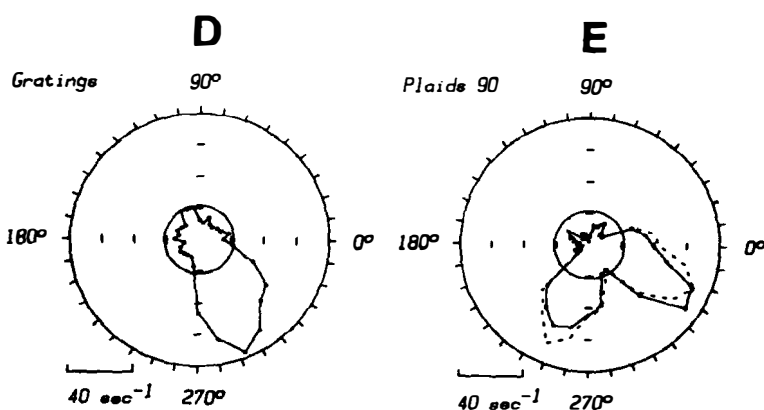
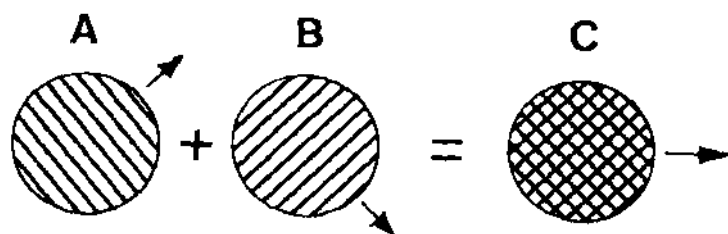
motion pathway, beginning with those that distinguish MT from V1 and subsequently proceeding to MST and area 7a. Although the motion pathway includes V2 (and probably other areas as well), physiological data are not yet available concerning the specific contributions of other areas to motion processing.

Motion of Complex Patterns

Visually guided behavior frequently depends on accurate information about the motion of complex patterns and objects. However, extraction of such information by the visual system is not as straightforward as it might seem. Consider for example the motion of the complex plaid pattern in Figure 6C. This plaid was created by superimposing the sinusoidal gratings in Figure 6A and 6B. The motion of each component grating is orthogonal to its orientation as indicated by the *arrows*. However, human observers viewing the plaid perceive rightward motion that is different from that of either oriented component (Adelson & Movshon 1982). The neuronal representation of the motion of the plaid is particularly interesting in light of the strongly orientation-selective responses of most V1 neurons. If motion sensitive neurons in V1 respond only to the oriented components of the plaid stimulus, their discharges will encode the motion of the component gratings (A and B) rather than the motion of the complex pattern (C). Because the motion of the pattern is the behaviorally relevant datum, the visual system must extract this information at higher levels of processing.

Movshon and colleagues (1986) have used the stimuli illustrated in Figure 6A–C to analyze the responses of direction-selective neurons in cat and monkey cortex. They found that while neurons in V1 encode the motion of the oriented components, a population of neurons in MT encodes the unitary motion of the entire pattern. The responses of each type

Figure 6 Direction selectivity for components and patterns in visual cortical neurons. A–C: Stimuli used to distinguish component direction selective responses from pattern direction selective responses. A sinusoidal grating moving upward and to the right (A) superimposed on a grating moving downward and to the right (B) results in a perception of a plaid pattern moving directly to the right (C). D–E: Direction tuning curves for a component direction selective neuron in cat striate cortex in response to a single sinusoidal grating (D) and a sinusoidal plaid (E). This neuron responded to the motion of the components of the plaid rather than to the unitary motion of the plaid itself (see text). This response pattern is typical of V1 neurons in cat and monkey. F–G: Direction tuning curves for a pattern direction selective neuron in macaque MT in response to a single grating (F) and plaid (G). This neuron responded to the unitary motion of the plaid pattern. The *dashed lines* in E and G indicate predicted tuning curves for a component direction selective response, assuming that the neurons respond to each component of the plaid in the same way that they respond to the single grating (D and F). Reprinted with permission from Movshon et al (1986).



of neuron are illustrated in Figure 6. Figure 6D is a polar plot of a direction tuning curve obtained from a V1 neuron by using a drifting sine wave grating as a stimulus. The neuron responded to a narrow range of directions down and to the right. Figure 6E illustrates the responses of the same neuron to the plaid pattern drifted through the receptive field in various directions. If the neuron were responsive to the unitary motion of the whole pattern, one would expect to obtain a tuning curve similar to that in Figure 6D. If, however, the neuron responded only to the individual motions of the components, the neuron should yield a bi-lobed tuning curve, responding first when the motion of the plaid is such that one component grating traverses the receptive field in the preferred direction and responding again when the motion of the other component grating is in the preferred direction. The responses illustrated in Figure 6E show that the neuron responded to the motion of the components and yielded no response when the unitary motion of the plaid was in the preferred direction. This type of response, termed "component direction selective," was characteristic of the V1 neurons tested by Movshon and colleagues (1986) in both cat and monkey, although the motion perceived by human observers was unambiguously that of the plaid.

In MT, however, about 20% of the neurons responded to the unitary motion of the plaid and were accordingly described as "pattern direction selective." Figure 6F illustrates the direction tuning curve obtained from one such MT neuron by using a single sine wave grating stimulus. In Figure 6G, the dotted bi-lobed tuning curve indicates the predicted response pattern for a component direction-selective neuron, but the data actually obtained (*solid curve*) show that this neuron responded optimally when the unitary motion of the plaid was in the neuron's preferred direction. Thus, pattern direction-selective neurons in MT encode information about the motion of complex patterns that is not signaled by single neurons in V1. The responses of these neurons are strikingly parallel to the perception of pattern motion by human observers.

Several investigators have observed neurons in MT whose preferred orientation for stationary slits is parallel to the preferred direction of motion (Baker et al 1981, Maunsell & Van Essen 1983a, Albright 1984), and Albright argued that these neurons are those identified as pattern direction-selective by Movshon and colleagues. This observation may bear on the mechanisms that generate pattern direction-selective responses and needs to be resolved experimentally. Another issue that must be addressed is the extent to which the ascending outputs of MT are characterized by pattern or component direction-selective responses. A firm assessment of the significance of this transformation will depend on how the newly encoded information is used within the visual system.

Speed Selectivity

The human visual system excels at extracting information about the speed of moving stimuli. Human observers reliably discriminate stimuli differing in speed by as little as 5% and maintain this capability across a broad range of speeds in all parts of the visual field (McKee 1981, McKee & Nakayama 1984). A simple hypothesis is that this perceptual capability is dependent on speed-tuned cortical neurons. However, several studies have shown that the speed tuning of single neurons in cat and monkey V1 varies substantially, depending on the spatial structure of the stimulus; their responses are not, therefore, invariant with respect to speed. Rather, V1 neurons are invariant in their responses to spatial and temporal frequency (Tolhurst & Movshon 1975, Holub & Morton-Gibson 1981, Bisti et al 1985, Foster et al 1985). For example, a neuron that responds preferentially to a sinusoidal grating of 4 cycles/deg will exhibit the same preferred spatial frequency regardless of the temporal drift rate at which the measurements are made. When tested with a temporal drift rate of 2 cycles/sec, therefore, this neuron will respond best to a speed of 0.5 deg/sec (speed = temporal frequency/spatial frequency), but it would respond best to a speed of 4 deg/sec were a temporal frequency of 16 cycles/sec used. Such neurons whose "preferred" speed changes with spatial and temporal frequency contrast strikingly to the performance of psychophysical observers who accurately judge the speed of sinusoidal gratings despite random variations in spatial and temporal frequency (McKee et al 1986).

Preliminary evidence indicates that in the monkey a small class of MT neurons responds in a manner that may account for the spatio-temporal independence of speed perception. Spatial and temporal tuning are not independent in these neurons, but covary so as to maintain a constant preferred speed over a broad range of spatial and temporal frequencies (Newsome et al 1983). Such neurons appear to represent a higher level of processing, where afferent neurons tuned to particular combinations of spatial and temporal frequency converge to build invariant responses to speed. Speed invariance may not be characteristic of all biological visual systems, however, because behavioral studies of the fly suggest that spatial and temporal tuning are entirely separable in its visual system (see Hildreth & Koch 1987 this volume).

Spatial Scale of Directional Interactions

A recent analysis of motion selectivity in monkey cortex by using stroboscopic stimuli revealed substantial differences in the spatial extent of directional interactions in V1 and MT (Mikami et al 1986a,b). In this study, a slit of light was stroboscopically stepped across the receptive field of

direction-selective neurons in both the preferred and null directions. The distance (spatial interval) and time (temporal interval) between successive flashes of the slit were systematically varied, and the responses were analyzed to determine the maximum spatial and temporal intervals for which direction selectivity could be obtained in each neuron.

The major findings were (a) that MT neurons maintained direction selectivity over spatial intervals that were, on the average, three times as large as those for V1 neurons at corresponding eccentricities, and (b) that MT and V1 neurons maintained direction selectivity over a similar range of temporal intervals. Consistent with these observations, MT neurons are direction selective for smooth motions of higher speeds ($\Delta x/\Delta t$) than V1 neurons. The maximum speed for direction selectivity to smooth motion is positively correlated with the maximum spatial interval in both MT and V1, and is twice as large (on the average) in MT as in V1 (Mikami et al 1986b). Preferred speeds are also higher in MT than in V1 (Figure 9 of Van Essen 1985). Thus, it appears that a major role of MT is to extend direction selectivity to a higher range of speeds by increasing the spatial scale of motion-sensing mechanisms. This trend may continue in cortical areas beyond MT. Preliminary observations on visually responsive neurons in Area 7a suggest that directional interactions can occur for spatial separations of 10–20 deg (Mountcastle et al 1984, Motter et al 1985). These values represent a substantial expansion of the spatial interactions underlying direction selectivity over those observed in MT.

The responses of cortical neurons to stroboscopic motion also suggest possible neural substrates for the phenomenon of apparent motion. Human observers perceive motion for successively flashed visual stimuli separated by appropriate spatial and temporal intervals (see review by Nakayama 1985). The spatio-temporal dependence of motion selectivity in MT neurons corresponded closely to that for perception of motion by human observers at high (8–32 deg/sec) apparent speeds, while both MT and V1 neurons were congruent with human performance at low (1–4 deg/sec) apparent speeds (Newsome et al 1986). It will be of interest to determine whether lesion studies confirm separable roles for V1 and MT over different ranges of speed in the manner suggested by the physiological experiments.

Surround Antagonism

It has recently become clear that the responses of many neurons in visual cortex can be greatly influenced by stimuli outside the classically defined receptive field. The classical receptive field is the region in which a single stimulus, such as a spot or bar, can evoke a response. Stimuli in the surrounding regions, by definition, cannot generate a response alone, but

can greatly modulate the response to a stimulus in the classical receptive field (reviewed by Allman et al 1985b). Several investigations have reported the existence of neurons whose responses to stimulus motion are modulated in a directionally antagonistic manner by motion in the surround (Sterling & Wickelgren 1969, Frost et al 1981, Frost & Nakayama 1983, von Grünau & Frost 1983). In monkeys, investigation has been directed toward MT and to a lesser extent, MST and V2. In owl monkey MT, Allman and colleagues (1985a) stimulated the classical receptive field with motion of a random dot pattern in the preferred direction while simultaneously stimulating a large surround region with a second random dot pattern. They found that for most MT neurons, the effects of surround stimulation on the responses to stimulation of the classical receptive field were dependent on the direction and speed of the surround pattern. The most common effect was the presence of an antagonistic, direction-selective surround that suppressed the response of a neuron to optimal stimulation of the classical receptive field when surround motion was in the same direction as motion in the classical receptive field. For many of these neurons, surround motion in the direction opposite that of classical receptive field motion facilitated the response to stimulation of the classical receptive field. Tanaka and colleagues (1986) observed similar effects in macaque MT. As yet, neurons in monkey V1 have not been examined for direction specific antagonistic surrounds. Whether such effects arise strictly from neuronal interactions in extrastriate cortex or whether such processing exists in V1 as well is not yet clear.

The antagonistic effects reported in these studies may play a role in a variety of visual functions requiring relative motion cues (see review by Allman et al 1985b). For example, MT neurons with antagonistic surrounds respond well to local motion within the classical receptive field, but not to global motion of extended textures or of the entire field. As such they are well suited for distinguishing a moving figure from background and for distinguishing object motion in the world from the global motion induced by a viewer's movement through the world.

Rotation

Tanaka, Saito and their colleagues recently found that the dorsal half of MST contains neurons selective for higher order motion phenomena such as rotation and changing size. These properties were not observed in MT (Tanaka et al 1986, Saito et al 1986). Neurons selective for the direction of rotatory motion have been reported previously in parietal cortex (Leinonen 1980, Sakata et al 1985, 1986), frontal cortex (Rizzolatti et al 1981), and the superior temporal polysensory area (STP) (Bruce et al 1981, Jeeves et al 1983). Fourteen percent of the MST neurons studied by Saito and

colleagues responded well to rotatory motion but not to linear movements of the same visual stimuli. Most responded selectively either to clockwise or to counterclockwise motion. Other tests showed that selectivity for rotation did not result from a preference for different directions of motion in different subregions of the receptive field, since small rotating texture patterns elicited the same response when placed in any portion of the receptive field. Neurons in both MST and area 7a are also reported to respond to rotations in depth, that is, in planes that are not perpendicular to the line of sight (Saito et al 1986, Sakata et al 1985, 1986). Rotation-selective neurons were not observed in the ventral half of MST, and this fact supports the argument that MST comprises two distinct visual areas (Desimone & Ungerleider 1986).

Rotation-selective responses constitute a property not evident at earlier stages in the motion pathway. However, because rotating patterns contain different linear velocities in different regions of the stimulus, it is possible that these neurons are simply responding to velocity shear. This issue needs to be addressed before selectivity for rotation per se is firmly established. Selectivity for rotation in depth is more problematic. The difficulty is that rotation of the visual displays in depth is accompanied by several cues such as changes in shape of the entire display. It is possible that an apparent selectivity for rotation in depth arises from selectivity for other cues that are not necessarily associated with rotation in depth. The use of random dot displays in which the degree of rotation may be smoothly varied while holding other cues invariant holds promise for addressing these issues.

Changing Size

Zeki (1974b) reported that neurons in MT of the macaque encode a monocular cue for motion in depth. These neurons responded preferentially to two edges moving in opposite directions within the receptive field. Because changing size is a potent cue for motion in depth, these neurons can provide a signal of motion toward (separating edges) or away from (approaching edges) the viewer. The cue is monocular because selective responses are obtained with stimulation of either eye alone. Similar response properties have been found in the extrastriate cortex of the cat (Regan & Cynader 1979).

Selectivity for changing size was found by Saito and colleagues (1986) in about 15% of MST neurons. They found that this response to changing size occurs within small subregions of the receptive field, thus showing that the mechanism for detecting changing size is reproduced continuously throughout the receptive field, as was the sensitivity for rotation described above. Control experiments indicated that the neurons respond poorly, if

at all, to unidirectional motion of the stimulus in the receptive field and that they did not respond to the changing light flux that accompanies changing size. These neurons seem to require simultaneous stimulation by motion in at least two different directions before emitting a substantial response. Thus the responses to changing size appear to represent another convergence of low-level motion cues to create higher level representations of important environmental events. Adaptation of neurons sensitive to changing size could account for the psychophysical observation that perception of changing size can be adapted independently of perception of simple linear stimulus motion (Regan & Beverly 1978a,b).

Opponent Vector Organization

Another major transformation in neuronal responses to visual motion is represented by "opponent vector" organization of receptive fields in area 7a (Motter & Mountcastle 1981) and in STP (Bruce et al 1981). Although the precise connections of 7a and STP with motion-related areas such as MT and MST are not yet established, some anatomical evidence suggests that both 7a and STP receive inputs from MST (see Desimone & Ungerleider 1986). Opponent vector neurons have large, frequently bilateral receptive fields in which the preferred direction of motion varies systematically from subregion to subregion within the receptive field. In one population of neurons the preferred directions are oriented relative to the fixation point so that each neuron responds best to motion toward the center of gaze regardless of the position of the stimulus in the receptive field. Another population responds best to motion away from the center of gaze. This type of response has not been observed in earlier levels of the motion pathway. Neurons with opponent vector responses (Motter & Mountcastle 1981, Mountcastle et al 1984) are likely to respond maximally to radial flow of the entire visual field either away from or toward the fixation point. Radial flow of this nature generally occurs as the animal moves through the environment, and such optical flow signals are known to be useful for perception of depth and as a cue for postural adjustment (see review by Nakayama 1985).

Motion-Related Behavioral Deficits

Recent studies employing small chemical lesions restricted to MT provided the first behavioral evidence for localization of motion analysis within extrastriate cortex. Newsome and colleagues (1985a) made small lesions in an identified portion of the topographic representation in MT, and observed selective (though transient) deficits in the monkey's use of visual motion to guide eye movements. When a moving target appeared in the affected portion of the visual field, both smooth pursuit eye movements

and saccadic eye movements were impaired in a manner suggesting underestimation of the speed of the moving target. The affected portion of the visual field corresponded to the topographic location at which the MT lesion was made; eye movements to targets in other regions were normal. In contrast, saccadic eye movements to stationary targets were normal at all points in the visual field including the region in which responses to moving targets were impaired. These effects of MT lesions were clearly different from those of restricted V1 lesions, which impaired eye movements to both moving and stationary targets (e.g. Mohler & Wurtz 1977, Goldberg et al 1982, Segraves et al 1983, Newsome et al 1985b).

These results were extended in a subsequent series of experiments in which Dürsteler and colleagues (1986) tested the effects of MT lesions on the pursuit of visual targets that were stabilized on the retina by using the monkey's eye position to move the target. MT lesions had no effect when the monkey pursued a target with a constant position error of one degree from the fovea. If, however, the experimenters added a constant velocity error to the stabilized image, MT lesions impaired the increase in eye speed with which the monkey normally responded to such velocity errors. Again, MT lesions had selective effects on the monkey's response to motion while leaving its response to static position unimpaired. (The implications of these results for visual control of the pursuit system are considered by Lisberger et al 1987, this volume.)

Wilson and colleagues (1977, 1979) examined the effects of suction ablations of MT in the bushbaby and the macaque. They concluded that animals with MT lesions were deficient in their ability to search visual space for behaviorally significant visual stimuli. While several aspects of these experiments pose difficulties for interpretation of the results (incomplete lesions, involvement of the optic radiation, lack of eye movement control), deficits in visuo-spatial search are broadly consistent with the known behavioral functions of parietal areas that are likely to receive inputs from the motion pathway. In another lesion study of cortex in the superior temporal sulcus, Collin & Cowey (1980) failed to find post-lesion deficits in movement detection thresholds. However, the lesions did not include all of MT, and the detection task may not have specifically tested the contributions of MT because it required no judgment about direction or speed of motion, parameters for which MT neurons are notably selective.

While lesion experiments are subject to serious pitfalls, the success of some of the experiments described above suggests that a more thorough behavioral analysis of the motion pathway may now be feasible. The discovery of several physiological transformations at higher levels of the pathway, coupled with apparent psychophysical correlates, has led to

specific hypotheses about the functional significance of these transformations. It is reasonable to anticipate that lesions of motion-related cortical areas in animals trained on appropriate psychophysical tasks will greatly clarify how physiological processing in these areas contributes to visual perception.

THE COLOR AND FORM PATHWAY

The color and form pathway has been less intensely studied than the motion pathway, but significant transformations of visual information have nonetheless been found within it. Several aspects of these transformations are similar to those seen in the motion pathway. For example, selectivities for basic stimulus parameters such as wavelength (deMonasterio & Schien 1982) or orientation (Desimone et al 1985) do not appear to increase along the color and form pathway. Also, retinotopic specificity decreases in successive levels of the color and form pathway: Compared to receptive fields in V1, fields in V4 are about 30 times larger (Van Essen & Zeki 1978, Maguire & Baizer 1984, Desimone & Gross 1985), and fields in AIT are well over 100 times larger (Desimone & Gross 1979). The similarities between the pathways suggest that the pathways use common computational strategies for processing information. In the sections that follow we consider evidence that the transformations along this pathway, like those in the motion pathway, are directed toward generating properties different and more complex than those that exist in earlier levels.

Although the transformations performed by the color and form pathway and the motion pathway may prove to be similar, the types of information that they process plainly differ. While color sensitivity is not readily observed in the motion pathway, high proportions of color selective neurons have been described in the blobs in V1, in the thin stripes in V2, and in V4. The percentage of color selective neurons reported for V4 has varied greatly between laboratories, due largely to differing criteria (see Desimone et al 1985, Van Essen 1985) and perhaps partly to the existence of distinct subdivisions within V4 (Zeki 1971, 1977, 1983c, Van Essen & Zeki 1978, Schein et al 1982, Maguire & Baizer 1984). While it was once thought that this area is primarily devoted to color analysis, it is now apparent that many V4 neurons lack color selectivity and are instead more sensitive to orientation or spatial frequency (Schein et al 1982, Desimone et al 1985). Little is known about the color specificity of neurons in the later stages of the color and form pathway to which V4 projects. Although neurons in AIT have been reported to distinguish different colors (Mikami & Kubota 1980, Fuster & Jervey 1982, Desimone et al 1984), these obser-

vations have generally been incidental, and no attempts have been made to control carefully for luminance or spectral content.

This pathway has been associated with form processing based in part on the orientation and spatial frequency selectivities that are prevalent in V1, V2, and V4. A continuation of form analysis in the inferotemporal areas is suggested by both neurophysiological and behavioral studies. Orientation selective neurons are found in PIT and AIT (Gross et al 1972, Desimone et al 1984), although their proportions are not yet established. These areas also contain neurons that are selective for other parameters relevant to the analysis of form, such as length, width, size, shape, and texture. As discussed above, lesions of the inferotemporal cortex cause deficits in discriminations of shape, size, or pattern.

Surround Mechanisms

Several distinctive physiological properties that exist in the color and form pathway appear to result from antagonistic surrounds. Receptive fields of V4 neurons have large surrounds that can greatly influence the responses to stimuli within the classically defined receptive field (Desimone & Schein 1983, Moran et al 1983, Schein et al 1983). Desimone and collaborators (1985) found that surround effects are often antagonistic and that they can show specificity for either the color or the spatial frequency of the surround stimulus. DeYoe and colleagues (1986) recently found a similar effect in V2, where neuronal responses are inhibited by patterns of oriented line segments in their surrounds only when the orientation of the segments matches the neuron's preferred orientation. Neurons with antagonistic, stimulus specific surrounds may contribute to discriminating figure from ground by responding to patterned objects on different backgrounds but not to uniformly patterned fields.

Von der Heydt et al (1984) tested the responses of neurons in macaque V1 and V2 to figures in which humans perceive illusory contours. Such figures are constructed so that an illusory edge or bar appears to span a region that is in fact blank. These investigators reported that when figures were positioned so that only the illusory contour entered a neuron's receptive field, some V2 neurons responded as though the contour were a real edge. V1 neurons did not respond to this stimulation. Although responses to an illusory contour depend on inputs from regions surrounding the classical receptive field, these inputs must differ from those mediating the surround effects described above because they are capable of driving neurons without direct stimulation of the classical receptive field. Responses to illusory contours therefore suggest that surround mechanisms may have greater scope than previously recognized.

Surround antagonism in the color and form pathway corresponds

closely to that described in the motion pathway and probably reflects a common computational strategy. Because the magnitude of surround effects has not been extensively examined in V1, it is not yet clear whether they play a major role in striate cortex as well. Although most research has focused on responses to stimulation of the classical receptive field, understanding the role of surrounds in shaping the visual response will undoubtedly represent an important area of study in the future.

Color Constancy

A perceptual capability that may depend on surround mechanisms is color constancy. In natural viewing conditions objects appear to have much the same color even when changes in illumination cause them to reflect light of different wavelength compositions (Jameson & Hurvich 1959, 1977, Land & McCann 1971, McCann et al 1976, Land 1977). The power of this compensating mechanism has been vividly demonstrated by Land using a montage of differently colored patches that he calls a "Mondrian" (see McCann et al 1976). The Mondrian is first illuminated with three projectors that emit narrow bandwidths of short, medium, and long wavelength light. Under these conditions the radiance of two of the patches, say a yellow and a green one, is measured to determine how much of each of the three illuminating wavelengths they reflect. The intensities of the three projectors are then individually adjusted so that the mixture of wavelengths reflected by the yellow patch precisely matches the mixture initially reflected by the green patch. If perceived color depended strictly on wavelength composition, the original yellow patch would now appear green. Instead, it still appears yellowish. This remarkable consistency in the perceived color does not occur if the surrounding colors are masked off and the patch is viewed in isolation. Thus, the perceived color of a surface is not a simple function of the wavelengths it reflects, but depends greatly on the wavelengths reflected by surrounding surfaces. Although this phenomenon has been referred to as color constancy, it should be noted that the compensating mechanism is not perfect. The perceived color may change somewhat under different lighting conditions, although it retains its basic hue.

Neurophysiological studies of visual cortex have largely neglected the distinction between wavelength composition and perceived color, leaving the neuronal basis of color constancy obscure. The mechanisms that generate this color compensation could in principle exist within the retina itself (Land 1977), but behavioral observations suggest that color constancy probably depends on the cerebral cortex (Land et al 1983). Recently Zeki (1980, 1983a,b) used a Mondrian stimulus to search for neuronal correlates of color constancy in macaque V1 and V4, and reported that neurons in V1 responded to the simple wavelength composition of stimuli, while

neurons in V4 appeared to signal the color perceived by a human observer. These intriguing observations are consistent with the notion that color constancy depends in part on transformations of signals that occur along the color and form pathway. However, there are alternative explanations for these results. The effects described in V4 depended on stimulating regions surrounding the classical receptive field (Zeki 1983a), but the surrounds of receptive fields in V1 were apparently not stimulated in an equivalent manner. Mondrian stimuli of fixed size were used to test neurons in both V1 and V4. Because receptive fields in V1 cover only about 1/30 the area of those in V4, a single patch of the Mondrian may have covered a critical region of the surround as well as the classical receptive field of the V1 neurons. The observed differences between V1 and V4 may therefore simply reflect differences in the spatial extent of receptive fields and their surrounds, rather than the appearance of a new property at the level of V4. Although the results of these experiments are of great interest, they must be interpreted cautiously until such issues are resolved.

Wild and colleagues (1985) made lesions in macaque monkeys that involved a restricted region of cortex including V4. The animals were impaired at discriminating colors under different illumination conditions, and these workers suggested that V4 is necessary for color constancy. While this is an attractive hypothesis, the data are not yet conclusive. V4 lesions also affect simple hue discrimination (Heywood & Cowey 1985), and the extent to which this impairment may affect performance on color constancy tasks is not known. Although much remains to be learned about the cortical contributions to color constancy, the recognition of a distinction between the wavelength composition and perceived color is likely to prove important in interpreting the neural representation of color in the later stages of visual cortex.

Face Selective Neurons

The later stages of the color and form pathway in PIT and AIT include many neurons whose stimulus preference is not immediately obvious: 40% of neurons in AIT have been reported to respond in a nonspecific manner to all visual stimuli (Desimone et al 1984). However, a comparable fraction appears to respond preferentially to particular complex objects, such as patterns, hands, or faces (Gross et al 1972, 1979, Rolls et al 1977, Ridley et al 1977, Bruce et al 1981, Rolls 1984, Perrett et al 1982, 1984, 1985, Baylis et al 1985). Neurons responding preferentially to complex visual objects have not been reported in the early stages of the color and form pathway. This implies a substantial transformation of the signals present at early levels and suggests that the inferotemporal cortex contributes to later stages of form analysis.

Among neurons that appear specific for complex objects, those selective for faces have attracted considerable attention. These neurons represent a small fraction of cells in the inferotemporal cortex (Desimone et al 1984), but they are apparently concentrated in a region in AIT near the fundus of the superior temporal sulcus, where as many as a quarter to a third of responsive neurons have been categorized as face selective (Desimone et al 1984, Rolls 1984, Perrett et al 1985). Neurons have been identified as face selective on the basis of a number of distinctive properties. Face selective neurons respond more strongly to faces than to other complex stimuli and generally do not respond to simple stimuli such as bars or gratings (Bruce et al 1981, Desimone et al 1984). They are sensitive to manipulations that affect the ability to identify a face, such as removing different facial features (Perrett et al 1982, Desimone et al 1984), yet most show no pronounced sensitivity to changes that have little effect on recognition (e.g. color, size, orientation, distance, spatial frequency content, direction of motion, or position within their receptive fields) (see Perrett et al 1982, Desimone et al 1984, Rolls 1984, Rolls et al 1985). Although face selective neurons generally respond to a variety of faces, the majority respond more or less strongly to particular faces (Perrett et al 1984, 1985, Rolls 1984, Baylis et al 1985).

Because faces are such complex patterns, it is difficult to prove conclusively that a neuron encodes information that is specifically related to faces. It is possible that these neurons are signaling information about either a broader class of complex objects or some simple pattern that is common to faces. However, demonstration that these neurons are sensitive to a variety of changes that adversely affect the identification of a face while being relatively insensitive to as many as seven other manipulations that do not alter recognition, presents a strong case that their activity conveys face related, and perhaps face specific information. Further characterization of the response properties of these neurons using systematic and repeatable stimulus manipulations will strengthen these findings. There is currently no physiological understanding of intermediate transformations by which face selective responses might be generated from the far simpler response properties described in early stages. Investigation of the processes that occur between these levels may improve our understanding of the functional role of these neurons.

Face selective cells are obvious candidates for contributing to the discrimination and identification of faces or individuals. The existence of these neurons does not, however, necessitate a theory of perception based on "grandmother" cells that are specific to one particular face (see Barlow 1972). There are simply too few neurons in the brain to represent the entire visual world in this way (Ballard et al 1983). In addition, computational

studies have shown that cortex-like mechanisms can identify complex patterns without using individual cells to signal particular objects (see Ballard 1986). In systems of this sort, a neuron might contribute to object identification by signaling a class of frequently encountered complex objects as opposed to specific instances of those objects. How the nervous system represents and recognizes particular visual objects remains one of the most formidable questions facing integrative neurophysiology.

EXTRARETINAL INPUTS

To date most investigations of information processing in visual cortex have been dominated by a strictly sensory perspective. Neurons have been described primarily as extracting and filtering different types of information from the visual scene. While this approach has contributed most of our current understanding of cortical function, neuronal activity in visual cortex is also influenced by other inputs that are not of direct retinal origin. Early studies of extraretinal inputs to visual neurons involved analysis of an "enhancement effect" in which visual responses were modulated by the animal's use of the stimulus: A neuron's response to a particular stimulus was stronger when a monkey attended to that stimulus than when the animal was attending elsewhere. Pronounced enhancement effects were observed in parietal cortex (Goldberg & Robinson 1977, Yin & Mountcastle 1977, 1978, Robinson et al 1978, Bushnell et al 1981), the frontal eye fields (Wurtz & Mohler 1976a, Goldberg & Bushnell 1981), and the superior colliculus (Goldberg & Wurtz 1972, Wurtz & Mohler 1976b).

Initial experiments in the early stages of macaque visual cortex, however, revealed no specific enhancement effects. Those neurons that did show an effect were modulated when the animal attended to any visual stimulus, thus suggesting that the change might simply reflect a level of arousal rather than a process specifically related to visual attention (see Wurtz et al 1980). Several studies support the idea that neurons in V1 are not strongly influenced by extraretinal inputs (Wurtz & Mohler 1976a, Hännny & Schiller 1986), but it has recently become clear that intermediate levels of visual cortex, like later stages, receive widespread and robust extraretinal inputs. For example, V4, only two stages removed from V1, has been shown to contain neurons with spatially selective enhancement effects similar to those previously demonstrated in the parietal cortex (Fischer & Boch 1981, 1985). It has also become obvious that extraretinal inputs are not restricted to modulating visual responses. Although a thorough survey of these inputs is beyond the scope of this review, the following examples

illustrate the prevalence and variety of extraretinal effects that can be found in the extrastriate cortex.

Moran & Desimone (1985) showed that neurons in V4 are influenced in a highly specific manner by attention. They found that if a red bar and a green bar were simultaneously flashed within the receptive field of a neuron that preferred red stimuli, the neuron responded well when the animal attended to the red bar but not when it attended to the non-preferred green bar. These results suggest that attention can, in effect, select a particular stimulus to be encoded by a neuron's response even though competing stimuli are simultaneously present in its receptive field. Extraretinal effects of this sort are common in V4: More than half the neurons tested showed attentional specificity. Other studies of this region of cortex have also found effects of attention that are specific to particular aspects of the stimuli (Braitman 1984, Hochstein & Maunsell 1985, Hännny & Schiller 1986).

A different type of extraretinal input was demonstrated by Fuster & Jervey (1982), who trained an animal to do a delayed match-to-sample task. At the start of each trial the animal was briefly cued with a color that he was required to remember during a delay period of more than 15 sec. At the end of the delay, several colors were presented and the animal had to select the one that had been cued. Among the neurons recorded in AIT were some whose rate of discharge during the delay depended on which color was cued. This difference in activity was not immediately related to a sensory input because no stimulus was present during the delay period. The activity during the delay appeared to encode task-specific information about the stimulus to which the animal should respond rather than signaling the presence of a visual stimulus.

Further indication that neurons in the visual cortex can encode task-specific information was found by Hännny et al (1986), who tested neurons in V4 by using a variation of the match-to-sample task in which an animal was required to match orientations. In these tests the animal was cued non-visually by having him feel the orientation of a grooved plate that he could not see. More than half the neurons in V4 responded in an orientation-selective fashion to the cue stimulus, although this information was not provided visually. Other experiments showed that these signals were also present if the orientation was cued visually before the start of each trial, and that they were not present when the animal felt the grooved plate while performing a task in which its orientation had no relevance. Thus it appears that many neurons in V4, like those in AIT, can convey signals that are not visual in any direct sense, but instead are related to a particular task.

In the motion pathway, preliminary investigations have found little or no evidence for extraretinal inputs to MT (Newsome & Wurtz 1981,

Wurtz et al 1984), but several such inputs exist in MST. Among the MST neurons exhibiting extraretinal effects, the neurons with signals related to pursuit eye movements are the best characterized. Visual tracking neurons were first reported in the parietal lobe by Hyvärinen & Poranen (1974) and by Mountcastle and colleagues (Mountcastle et al 1975; Lynch et al 1977). Robinson and colleagues (1978) found that many tracking neurons received strong visual inputs and suggested that the tracking responses could be explained solely on the basis of retinal signals. This was shown to be the case for many tracking neurons in area 7a (Sakata et al 1983), but a population of neurons located in and around MST in the depths of the superior temporal sulcus receive an extraretinal input related to pursuit eye movements in addition to their visual inputs (Sakata et al 1983, 1985, Kawano et al 1984, Kawano & Sasaki 1984, Wurtz et al 1984). This pursuit signal cannot be explained by passive visual properties because it exists during short intervals of pursuit in total darkness (Sakata et al 1983) and during pursuit of stabilized retinal images (Wurtz & Newsome 1985). Rather, the pursuit signal results from extraretinal inputs and may provide an internal representation of eye velocity (Kawano et al 1984).

A final example of extraretinal influences on visual responses are recent findings in area 7a that suggest a mechanism for representing the visual world in stable, head-centered coordinates. In earlier stages of the visual pathway, visual space is represented in retinotopic coordinates so that the cortical representation of a stationary object changes with each eye movement. Most motor acts, however, are directed toward locations in space. Andersen & Mountcastle (1983) have examined neurons in area 7a that are visually responsive, with discrete (though large) receptive fields in which the strength of the visual response depends on the direction in which the monkey's eyes point. Because a neuron will not respond unless the eyes point in a particular direction *and* a stimulus falls on a particular retinal region, a neuron will be strongly driven only by visual stimuli within a restricted range of locations in head-centered space. By combining the activity of neurons that respond to a common location in space but for a wide range of eye positions, an eye-position independent representation of visual space can be achieved (Andersen et al 1985). As yet there is no evidence that neuronal activity is combined in this manner in single neurons, but the aggregate activity of neurons in area 7a encodes the necessary information.

Collectively, these examples show that extraretinal signals exist in many extrastriate visual areas and appear to play a role that goes beyond simple modulation of visual signals. It is likely that extraretinal signals represent a substantial component of the information present in extrastriate cortex of the behaving animal. While the anesthetized preparation has certain

advantages, many cortical signals are observable only in alert animals. Further insight about this largely unexplored dimension of cortical activity is likely to be essential for understanding the function of extrastriate visual cortex.

CONCLUDING COMMENTS

Several new insights about information flow and processing in the extrastriate cortex have emerged in the last few years. The current notion of cortical streams of visual processing is a modification of the proposal by Zeki (1975, 1978) that extrastriate areas operate in parallel, with each area processing a different type of information. Evidence now suggests that the organization of cortical visual areas encompasses both parallel and serial relationships. Visual cortex appears to contain parallel streams of processing that consist of serially connected areas, with each area representing a different level of processing. The case for serial processing in extrastriate cortex is supported both by the pattern of ascending and descending anatomical connections in the cortical hierarchy (Figure 4) and the increasingly complex properties of neurons at successive stages of each stream of processing.

While the concept of streams introduces a serial aspect to the organization of extrastriate visual areas, it would be incorrect to view processing within a stream as a strictly sequential set of operations. Anatomical experiments indicate that processing within each stream is not completely serial. More elaborate forms of processing are suggested both by the projections that skip levels within a stream and by the ubiquitous feedback connections. Anatomical and physiological evidence for interconnections between the streams also points to more complex interactions. While much remains to be learned about the functional implications of streams of processing, the identification of a level of organization between that of individual cortical areas and the entire visual cortex should help considerably in evaluating the cortical processes underlying vision.

A major need for future research is to identify additional transformations of visual information in the extrastriate cortex. The transformations that have been observed to date probably represent only a small fraction of the total. Impetus for discovery of new physiological transformations is likely to come from visual psychophysics and computational neuroscience. Studies of properties such as pattern direction selectivity in MT illustrate the potential for contributions from psychophysical and computational approaches. Psychophysics yields important information concerning the response of the entire visual system to complex stimuli, and can provide valuable hints about the types of trans-

formations and signals that occur in visual cortex. Computational studies attempt to specify rigorously the computational steps required to implement a particular capability, and can suggest neuronal operations that might be necessary. Simulations of such operations may help us deduce the significance of signals encoded in cortical neurons. We expect that interactions with these disciplines will become increasingly valuable as physiologists pursue higher-order aspects of integrative neural function.

Finally, investigation of extraretinal signals in the visual cortex is likely to become an area of particular interest in the future. Robust extraretinal signals are apparently common in most extrastriate visual areas, suggesting that they represent a fundamental aspect of cortical processing. We currently have only the most basic understanding of these extraretinal inputs. Many questions remain unanswered about the origin of extraretinal signals and their flow within visual cortex. More intriguing still are questions about how extraretinal signals interact with visual signals in cortex. Although systematic investigation of these interactions poses many challenges, both in the execution of experiments and in the interpretation of results, information about this aspect of cortical function may ultimately prove essential to understanding the neural processes leading to visual perception.

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Literature Cited

- Adelson, M., Movshon, J. A. 1982. Phenomenal coherence of moving visual patterns. *Nature* 300: 523-25
- Albright, T. D. 1984. Direction and orientation selectivity of neurons in visual area MT of the macaque. *J. Neurophysiol.* 52: 1106-30
- Allman, J. M., Kaas, J. H. 1971. A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*). *Brain Res.* 31: 85-105
- Allman, J. M., Kaas, J. H. 1974a. The organization of the second visual area (V II) in the owl monkey: A second order transformation of the visual hemifield. *Brain Res.* 76: 247-65
- Allman, J. M., Kaas, J. H. 1974b. A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey (*Aotus trivirgatus*). *Brain Res.* 81: 199-213
- Allman, J. M., Kaas, J. H. 1975. The dorso-medial cortical visual area: A third tier area in the occipital lobe of the owl monkey (*Aotus trivirgatus*). *Brain Res.* 100: 473-87
- Allman, J. M., Kaas, J. H. 1976. Representation of the visual field on the medial wall of occipital-parietal cortex in the owl monkey. *Science* 191: 572-75
- Allman, J. M., Meizin, F., McGuinness, E.

- 1985a. Direction and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception* 14: 105-26
- Allman, J. M., Meizin, F., McGuinness, E. 1985b. Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. *Ann. Rev. Neurosci.* 8: 407-30
- Andersen, R. A., Essick, G. K., Siegel, R. M. 1985. The encoding of spatial location by posterior parietal neurons. *Science* 230: 456-58
- Andersen, R. A., Mountcastle, V. B. 1983. The influence of the angle of gaze upon the excitability of the light-sensitive neurons of the posterior parietal cortex. *J. Neurosci.* 3: 532-48
- Baker, J. F., Petersen, S. E., Newsome, W. T., Allman, J. M. 1981. Visual response properties of neurons in four extrastriate visual areas of the owl monkey (*Aotus trivirgatus*). *J. Neurophysiol.* 45: 397-416
- Barlow, H. 1972. Single units and sensation: A neuron doctrine for perceptual psychology? *Perception* 1: 371-94
- Ballard, D. H. 1986. Cortical connections and parallel processing: Structure and function. *Behav. Brain Sci.* 9: 67-120
- Ballard, D. H., Hinton, G. E., Sejnowski, T. J. 1983. Parallel visual computation. *Nature* 306: 21-26
- Baylis, G. C., Rolls, E. T., Leonard, C. M. 1985. Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. *Brain Res.* 342: 91-102
- Bisti, S., Carmignoto, G., Galli, L., Maffei, L. 1985. Spatial-frequency characteristics of neurons of area 18 in the cat: Dependence on the velocity of the visual stimulus. *J. Physiol.* 359: 259-68
- Blasdel, G. G., Fitzpatrick, D. 1984. Physiological organization of layer 4 in macaque striate cortex. *J. Neurosci.* 4: 880-95
- Braitman, D. J. 1984. Activity of neurons in monkey posterior temporal cortex during multidimensional visual discrimination tasks. *Brain Res.* 307: 17-28
- Bruce, C. J., Desimone, R., Gross, C. G. 1981. Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *J. Neurophysiol.* 46: 369-84
- Buchbinder, S., Dixon, B., Hwang, Y. W., May, J. G., Glickstein, M. 1980. The effects of cortical lesions on visual guidance of the hand. *Soc. Neurosci. Abstr.* 6: 675
- Burkhalter, A., Felleman, D. J., Newsome, W. T., Van Essen, D. C. 1986. Anatomical and physiological asymmetries related to visual areas V3 and VP in macaque extrastriate cortex. *Vision Res.* 26: 63-80
- Bushnell, M. C., Goldberg, M. E., Robinson, D. L. 1981. Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. *J. Neurophysiol.* 46: 755-72
- Cavanagh, P., Tyler, C. W., Favreau, O. E. 1984. Perceived velocity of moving chromatic gratings. *J. Opt. Soc. Am.* 1: 893-99
- Collin, N. G., Cowey, A. 1980. The effect of ablation of frontal eye-fields and superior colliculi on visual stability and movement discrimination in rhesus monkeys. *Exp. Brain Res.* 40: 251-60
- Cowey, A. 1979. Cortical maps and visual perception. *Q. J. Exp. Psychol.* 31: 1-17
- Cragg, B. G. 1969. The topography of the afferent projections in circumstriate visual cortex of the monkey studied by the Nauta method. *Vision Res.* 9: 733-47
- Damasio, A. R., Benton, A. L. 1979. Impairments of hand movements under visual guidance. *Neurology* 29: 170-8
- Damasio, A. R., Damasio, H., Van Hoesen, G. W. 1982. Prosopagnosia: Anatomical basis and behavioral mechanisms. *Neurology* 32: 331-41
- Dean, P. 1976. Effects of inferotemporal lesions on the behavior of monkeys. *Psychol. Bull.* 83: 41-71
- Dean, P. 1982. Visual behavior in monkeys with inferotemporal lesions. See Ingle et al 1982, pp. 587-628
- deMonasterio, F. M., Schein, S. J. 1982. Spectral bandwidths of color-opponent cells of geniculocortical pathway of macaque monkeys. *J. Neurophysiol.* 47: 214-24
- Derrington, A. M., Lennie, P. 1984. Spatial and temporal contrast sensitivities of neurons in lateral geniculate nucleus of macaque. *J. Physiol.* 357: 219-40
- Derrington, A. M., Krauskopf, J., Lennie, P. 1984. Chromatic mechanisms in lateral geniculate nucleus of macaque. *J. Physiol.* 357: 241-65
- Desimone, R., Albright, T. D., Gross, C. G., Bruce, C. 1984. Stimulus-selective properties of inferior temporal neurons in the macaque. *J. Neurophysiol.* 4: 2051-62
- Desimone, R., Fleming, J., Gross, C. G. 1980. Prestriate afferents to inferotemporal cortex: An HRP study. *Brain Res.* 184: 41-55
- Desimone, R., Gross, C. G. 1979. Visual areas in the temporal cortex of the macaque. *Brain Res.* 178: 363-80
- Desimone, R., Schein, S. J. 1983. Receptive field properties of neurons in visual area

- V4 of the macaque. *Soc. Neurosci. Abstr.* 9: 153
- Desimone, R., Schein, S. J., Moran, J., Ungerleider, L. G. 1985. Contour, color and shape analysis beyond the striate cortex. *Vision Res.* 25: 441-52
- Desimone, R., Ungerleider L. G. 1986. Multiple visual areas in the caudal superior temporal sulcus of the macaque. *J. Comp. Neurol.* 248: 164-89
- DeYoe, E. A., Knierim, J., Sagi, D., Julesz, B., Van Essen, D. C. 1986. Single unit responses to static and dynamic texture patterns in macaque V2 and V1 cortex. *Invest. Ophthalmol. Vis. Sci.* 27: 18
- DeYoe, E. A., Van Essen, D. C. 1985. Segregation of efferent connections and receptive field properties in visual area V2 of the macaque. *Nature* 317: 58-61
- Dow, B. M. 1974. Functional classes of cells and their laminar distribution in monkey visual cortex. *J. Neurophysiol.* 37: 927-46
- Dubner, R., Zeki, S. M. 1971. Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus. *Brain Res.* 35: 528-32
- Dürsteler, M., Wurtz, R. H., Newsome, W. T. 1986. Directional and retinotopic pursuit deficits following lesions of the foveal representation within the superior temporal sulcus of the macaque monkey. *J. Neurophysiol.* In press
- Edelman, G. M., Gall, W. E., Cowan, W. M., eds. 1984. *Dynamic Aspects of Neocortical Function*. New York: Wiley
- Felleman, D. J., Kaas, J. H. 1984. Receptive-field properties of neurons in middle temporal visual area (MT) of owl monkeys. *J. Neurophysiol.* 52: 488-513
- Fischer, B., Boch, R. 1981. Selection of visual targets activates prelunate cortical cells in rhesus monkey. *Exp. Brain Res.* 41: 431-33
- Fischer, B., Boch, R. 1985. Peripheral attention versus central fixation: Modulation of the visual activity of prelunate cortical cells of the rhesus monkey. *Brain Res.* 345: 111-23
- Fitzpatrick, D., Lund, J. S., Blasdel, G. G. 1985. Intrinsic connections of macaque striate cortex: Afferent and efferent connections of lamina 4C. *J. Neurosci.* 5: 3329-49
- Foster, K. H., Gaska, J. P., Nagler, M., Pollen, D. A. 1985. Spatial and temporal frequency selectivity of neurones in visual cortical areas V1 and V2 of the macaque monkey. *J. Physiol.* 365: 331-63
- Friedman, D. P. 1983. Laminar patterns of termination of cortico-cortical afferents in the somatosensory system. *Brain Res.* 273: 147-51
- Frost, B. J., Nakayama, K. 1983. Single visual neurons code opposing motion independent of direction. *Science* 220: 774-75
- Frost, B. J., Scilley, P. L., Wong, S. C. P. 1981. Moving background patterns reveal double-opponency of directionally specific pigeon tectal neurons. *Exp. Brain Res.* 43: 173-85
- Fuster, J. M., Jervey, J. P. 1982. Neuronal firing in the inferotemporal cortex of the monkey in a visual memory task. *J. Neurophysiol.* 2: 361-75
- Gattass, R., Gross, C. G. 1981. Visual topography of striate projection zone (MT) in posterior superior temporal sulcus of the macaque. *J. Neurophysiol.* 46: 621-38
- Goldberg, M. E., Bruce, C. J., Ungerleider, L., Mishkin, M. 1982. Role of the striate cortex in generation of smooth pursuit eye movements. *Neurology* 12: 113
- Goldberg, M. E., Bushnell, M. C. 1981. Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye field specifically related to saccades. *J. Neurophysiol.* 46: 773-87
- Goldberg, M. E., Robinson, D. L. 1977. Visual responses of neurons in monkey inferior parietal lobule: The physiological substrate of attention and neglect. *Neurology* 27: 350
- Goldberg, M. E., Wurtz, R. H. 1972. Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. *J. Neurophysiol.* 35: 560-74
- Gross, C. G. 1973a. Visual functions of inferotemporal cortex. In *Handb. Sensory Physiol.* 7(3): 451-82
- Gross, C. G. 1973b. Inferotemporal cortex and vision. *Prog. Physiol. Psychol.* 5: 77-123
- Gross, C. G., Bender, D. B., Gerstein, G. L. 1979. Activity of inferior temporal neurons in behaving monkeys. *Neuropsychology* 17: 215-29
- Gross, C. G., Bruce, C. J., Desimone, R., Fleming, J., Gattass, R. 1981. Cortical visual areas of the temporal lobe. See Woolsey 1981, 2: 187-216
- Gross, C. G., Rocha-Miranda, C. E., Bender, D. B. 1972. Visual properties of neurons in inferotemporal cortex of the macaque. *J. Neurophysiol.* 35: 96-111
- Häenny, P. E., Maunsell, J. H. R., Schiller, P. H. 1986. State dependent activity in monkey visual cortex: II. Visual and non-visual factors in V4. Submitted
- Häenny, P. E., Schiller, P. H. 1986. State dependent activity in monkey visual cortex: I. Effects in V1 and V4. Submitted
- Heywood, C. A., Cowey, A. 1985. Disturbances of pattern and hue dis-

- crimination following removal of the "colour" area in primates. *Neurosci. Lett.* 21: S11
- Hildreth, E. C., Koch, C. 1987. The analysis of visual motion: From computational theory to neuronal mechanisms. *Ann. Rev. Neurosci.* 10: 477-533
- Hochstein, S., Maunsell, J. H. R. 1985. Dimensional attention effects in the responses of V4 neurons of the macaque monkeys. *Soc. Neurosci. Abstr.* 11: 1244
- Holub, R. A., Martin-Gibson, M. 1981. Response of visual cortical neurons of the cat to moving sinusoidal gratings: Response-contrast functions and spatio-temporal interactions. *J. Neurophysiol.* 46: 1244-59
- Horton, J. C., Hubel, D. H. 1980. Cytochrome oxidase stain preferentially labels intersections of ocular dominance and vertical orientation columns in macaque striate cortex. *Soc. Neurosci. Abstr.* 6: 315
- Hubel, D. H., Livingstone, M. S. 1985. Complex-unoriented cells in a subregion of primate area 18. *Nature* 315: 325-27
- Hubel, D. H., Wiesel, T. N. 1972. Laminar and columnar distribution of geniculocortical fibers in macaque monkey. *J. Comp. Neurol.* 146: 421-50
- Hubel, D. H., Wiesel, T. N. 1977. Functional architecture of macaque monkey visual cortex. *Proc. R. Soc. London Ser. B* 198: 1-59
- Humphrey, A. L., Hendrickson, A. E. 1980. Radial zones of high metabolic activity in squirrel monkey striate cortex. *Soc. Neurosci. Abstr.* 6: 315
- Hyvärinen, J., Poranen, A. 1974. Function of parietal associative area 7 as revealed from cellular discharges in alert monkeys. *Brain* 97: 673-92
- Ingle, D. J., Goodale, M. A., Mansfield, R. J. W. 1982. *Analysis of Visual Behavior*. Cambridge, Mass.: MIT Press
- Iwai, E. 1981. Visual mechanisms in the temporal and prestriate association cortices of the monkey. *Adv. Physiol. Sci.* 17: 279-86
- Iwai, E. 1985. Neuropsychological basis of pattern vision in macaque monkeys. *Vision Res.* 25: 425-39
- Jameson, D., Hurvich, L. M. 1959. Perceived color and its dependence on focal, surrounding, and preceding stimulus variables. *J. Opt. Soc. Am.* 49: 890-98
- Jameson, D., Hurvich, L. M. 1977. Color adaptation: Sensitivity, contrast, after-images. In *Handb. Sensory Physiol.* 7(4): 568-81
- Jeeves, M. A., Milner, A. D., Perrett, D. I., Smith, P. A. J. 1983. Visual cells responsive to direction of motion and stimulus form in the anterior superior temporal sulcus of the macaque monkey. *Proc. Roy. Soc. London Ser. B* 341: 80P
- Jones, E. G., Coulter, J. D., Hendry, S. H. C. 1978. Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. *J. Comp. Neurol.* 181: 291-348
- Jones, E. G., Powell, T. P. S. 1970. An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. *Brain* 93: 793-802
- Jones, E. G., Wise, S. P. 1977. Size, laminar and columnar distribution of efferent cells in the sensory motor cortex of monkeys. *J. Comp. Neurol.* 175: 391-438
- Joynt, R. J., Honch, G. W., Rubin, A. J., Trudell, R. G. 1985. Occipital lobe syndromes. *Handb. Clinical Neurol.* 1: 45-62
- Kaas, J. H. 1978. The organization of visual cortex in primates. In *Sensory Systems of Primates*, ed. C. R. Noback, pp. 151-79. New York: Plenum
- Kawano, K., Sasaki, M., Yamashita, M. 1984. Response properties of neurons in posterior parietal cortex of monkey during visual-vestibular stimulation. I. Visual tracking neurons. *J. Neurophysiol.* 51: 340-51
- Kawano, K., Sasaki, M. 1984. Response properties of neurons in posterior parietal cortex of monkey during visual-vestibular stimulation. II. Optokinetic neurons. *J. Neurophysiol.* 51: 352-60
- Kuffler, S. W. 1953. Discharge patterns and functional organization of mammalian retina. *J. Neurophysiol.* 16: 37-68
- Land, E. H. 1977. The retinex theory of color vision. *Sci.* 237(6): 108-28
- Land, E. H., McCann, J. J. 1971. Lightness and retinex theory. *J. Opt. Soc. Am.* 61: 1-11
- Land, E. H., Hubel, D. H., Livingstone, M. S., Perry, S. H., Burns, M. M. 1983. Colour-generating interactions across the corpus callosum. *Nature* 303: 616-18
- Leichnetz, G. R. 1980. An interhemispheric columnar projection between two cortical multi-sensory convergence areas (inferior parietal lobule and prefrontal cortex): An anterograde study in macaque using HRP gel. *Neurosci. Lett.* 18: 119-24
- Leinonen, L. 1980. Functional properties of neurons in the posterior part of area 7 in awake monkeys. *Acta Physiol. Scand.* 108: 301-8
- Lisberger, S. G., Morris, E. J., Tychsen, L. 1987. Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Ann. Rev. Neurosci.* 10: 97-129
- Livingstone, M. S., Hubel, D. H. 1984. Anatomy and physiology of a color system in

- the primate visual cortex. *J. Neurosci.* 4: 309–56
- Lund, J. S., Boothe, R. G. 1975. Interlaminar connections and pyramidal neuron organisation in the visual cortex, area 17, of the macaque monkey. *J. Comp. Neurol.* 159: 305–34
- Lynch, J. C., Mountcastle, V. B., Talbot, W. H., Yin, T. C. T. 1977. Parietal lobe mechanisms for directed visual attention. *J. Neurophysiol.* 40: 362–89
- Macko, K. A., Jarvis, C. D., Kennedy, C., Miyaoka, M., Shinohara, M., Sokoloff, L., Mishkin, M. 1982. Mapping the primate visual system with [2-14C] deoxyglucose. *Science* 218: 394–97
- Maguire, W. M., Baizer, J. S. 1984. Visuotopic organization of the prelunate gyrus in rhesus monkey. *J. Neurosci.* 4: 1690–1704
- Maunsell, J. H. R. 1986. Physiological evidence for two visual systems. In *Matters of Intelligence*, ed. L. Vaina. Dordrecht: Reidel. In press
- Maunsell, J. H. R., Van Essen, D. C. 1983a. Functional properties of neurons in the middle temporal visual area (MT) of the macaque monkey: I. Selectivity for stimulus direction, speed and orientation. *J. Neurophysiol.* 49: 1127–47
- Maunsell, J. H. R., Van Essen, D. C. 1983b. Functional properties of neurons in the middle temporal visual area (MT) of the macaque monkey: II. Binocular interactions and the sensitivity to binocular disparity. *J. Neurophysiol.* 49: 1148–67
- Maunsell, J. H. R., Van Essen, D. C. 1983c. The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *J. Neurophysiol.* 3: 2563–86
- Mayhew, J. E. W., Anstis, S. M. 1972. Movement after-effects contingent on color, intensity, and pattern. *Percept. Psychobiol.* 12: 77–85
- McCann, J. J., McKee, S. P., Taylor, R. H. 1976. Quantitative studies in retinex theory. *Vision Res.* 16: 445–58
- McKee, S. P. 1981. A local mechanism for differential velocity detection. *Vision Res.* 21: 491–500
- McKee, S. P., Nakayama, K. 1984. The detection of motion in the peripheral visual field. *Vision Res.* 24: 25–32
- McKee, S. P., Silverman, G. H., Nakayama, K. 1986. Precise velocity discrimination despite random variations in temporal frequency and contrast. *Vision Res.* In press
- Meadows, J. C. 1974a. Disturbed perception of colours associated with localized cerebral lesions. *Brain* 97: 615–32
- Meadows, J. C. 1974b. The anatomical basis of prosopagnosia. *J. Neurol. Neurosurg. Psychiatr.* 37: 489–501
- Mesulam, M. M., Van Hoesen, G. W., Pandya, D. N., Geschwind, N. 1977. Limbic and sensory connections of the inferior parietal lobule (area PG) in the rhesus monkey: A study with a new method for horseradish peroxidase histochemistry. *Brain Res.* 136: 393–414
- Michael, C. R. 1985. Laminar segregation of color cells in the monkey striate cortex. *Vision Res.* 25: 415–23
- Mikami, A., Kubota, K. 1980. Inferotemporal neuron activities during color discrimination with delay. *Brain Res.* 182: 65–78
- Mikami, A., Newsome, W. T., Wurtz, R. H. 1986. Motion selectivity in macaque visual cortex: I. Mechanisms of direction and speed selectivity in extrastriate area MT. *J. Neurophysiol.* 55: 1308–27
- Mikami, A., Newsome, W. T., Wurtz, R. H. 1986b. Motion selectivity in macaque visual cortex: II. Spatio-temporal range of directional interactions in MT and VI. *J. Neurophysiol.* 55: 1328–39
- Mishkin, M., Ungerleider, L. G., Macko, K. A. 1983. Object vision and spatial vision: Two cortical pathways. *Trends Neurosci.* 6: 414–17
- Mohler, C. W., Wurtz, R. H. 1977. Role of striate cortex and superior colliculus in visual guidance of saccadic eye movements in monkeys. *J. Neurophysiol.* 40: 74–94
- Moran, J., Desimone, R. 1985. Selective attention gates visual processing in the extrastriate cortex. *Science* 229: 782–84
- Moran, J., Desimone, R., Schein, S. J., Mishkin, M. 1983. Suppression from ipsilateral visual field in area V4 of the macaque. *Soc. Neurosci. Abstr.* 9: 957
- Motter, B. C., Steinmetz, M. A., Mountcastle, V. B. 1985. Directional sensitivity of parietal visual neurons to moving stimuli depends upon the extent of the field traversed by the moving stimuli. *Soc. Neurosci. Abstr.* 11: 1011
- Motter, B. C., Mountcastle, V. B. 1981. The functional properties of the light-sensitive neurons of the posterior parietal cortex studied in waking monkeys: Foveal sparing and opponent vector organization. *J. Neurosci.* 1: 3–26
- Mountcastle, V. B., Lynch, J. C., Georgopoulos, A., Sakata, H., Acuna, C. 1975. Posterior parietal association cortex of the monkey: Command function for operations within extrapersonal space. *J. Neurophysiol.* 38: 871–908
- Mountcastle, V. B., Motter, B. C., Steinmetz, M. A., Duffy, J. 1984. Looking and seeing: The visual functions of the parietal lobe. See Edelman et al 1984, pp. 159–93
- Movshon, J. A., Adelson, E. H., Gizzi, M.

- S., Newsome, W. T. 1986. The analysis of moving visual patterns. In *Pattern Recognition Mechanisms*, ed. C. Chagas, R. Gattass, C. Gross, pp. 117–51. New York: Springer-Verlag
- Movshon, J. A., Newsome, W. T. 1984. Functional characteristics of striate cortical neurons projecting to MT in the macaque. *Soc. Neurosci. Abstr.* 10: 933
- Nakayama, K. 1985. Biological image motion processing: A review. *Vision Res.* 25: 625–60
- Newsome, W. T., Gizzi, M. S., Movshon, J. A. 1983. Spatial and temporal properties of neurons in macaque MT. *Invest. Ophthalmol. Vis. Sci.* 24: 106
- Newsome, W. T., Mikami, A., Wurtz, R. H. 1986. Motion selectivity in macaque visual cortex. III. Psychophysics and physiology of apparent motion. *J. Neurophysiol.* 55: 1340–51
- Newsome, W. T., Wurtz, R. H. 1981. Response properties of single neurons in the middle temporal visual area (MT) of alert macaque monkeys. *Soc. Neurosci. Abstr.* 7: 832
- Newsome, W. T., Wurtz, R. H., Dürsteler, M. R., Mikami, A. 1985a. Deficits in visual motion perception following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *J. Neurosci.* 5: 825–40
- Newsome, W. T., Wurtz, R. H., Dürsteler, M. R., Mikami, A. 1985b. Punctate chemical lesions of striate cortex in the macaque monkey: Effect on visually guided saccades. *Exp. Brain Res.* 58: 392–99
- Pearlman, A. L., Birch, J., Meadows, J. C. 1979. Cerebral color blindness: An acquired defect in hue discrimination. *Ann. Neurol.* 5: 253–61
- Perrett, D. I., Rolls, E. T., Caan, W. 1982. Visual neurons responsive to faces in the monkey temporal cortex. *Exp. Brain Res.* 47: 329–42
- Perrett, D. I., Smith, P. A. J., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., Jeeves, M. A. 1984. Neurons responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception. *Human Neurobiol.* 3: 197–208
- Perrett, D. I., Smith, P. A. J., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., Jeeves, M. A. 1985. Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proc. R. Soc. London Ser. B* 223: 293–317
- Peters, A., Jones, E. G., eds. 1985. *Cerebral Cortex*. New York: Plenum
- Petersen, S. E., Baker, J. F., Allman, J. M. 1980. Dimensional selectivity of neurons in the dorsolateral visual area of the owl monkey. *Brain Res.* 197: 507–11
- Poggio, G. F., Fischer, B. 1977. Binocular interactions and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. *J. Neurophysiol.* 40: 1392–1405
- Poggio, G. F., Poggio, T. 1984. The analysis of stereopsis. *Ann. Rev. Neurosci.* 7: 379–412
- Pohl, W. 1973. Dissociation of spatial discrimination deficits following frontal and parietal lesions in monkeys. *J. Comp. Physiol. Psychol.* 82: 227–39
- Ramachandran, V. S., Gregory, R. L. 1978. Does colour provide an input to human motion perception? *Nature* 275: 55–56
- Ratcliff, G., Davies-Jones, G. A. B. 1972. Defective visual localization in focal brain wounds. *Brain* 95: 49–60
- Regan, D., Beverly, K. 1978a. Illusory motion in depth: After-effect of adaptation to changing size. *Vision Res.* 18: 209–12
- Regan, D., Beverly, K. 1978b. Looming detectors in the human visual pathway. *Vision Res.* 18: 415–21
- Regan, D., Cynader, M. 1979. Neurons in area 18 of cat visual cortex selectively sensitive to changing size: Nonlinear interactions between responses to two edges. *Vision Res.* 19: 699–711
- Ridley, R. M., Hester, N. S., Ettlinger, G. 1977. Stimulus- and response-dependent units from the occipital and temporal lobes of the unanaesthetized monkey performing learnt visual tasks. *Exp. Brain Res.* 27: 539–52
- Rizzolatti, G., Scandolara, C., Matelli, M., Gentilucci, M. 1981. Afferent properties of periarculate neurons in macaque monkeys. II. Visual responses. *Behav. Brain Res.* 2: 147–63
- Robinson, D. L., Goldberg, M. E., Stanton, G. B. 1978. Parietal association cortex in the primate: Sensory mechanisms and behavioral modulations. *J. Neurophysiol.* 41: 910–32
- Rockland, K. S., Pandya, D. N. 1979. Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. *Brain Res.* 179: 3–20
- Rolls, E. T., Baylis, G. C., Leonard, C. M. 1985. Role of low and high spatial frequencies in the face-selective responses of neurons in the cortex in the superior temporal sulcus in the monkey. *Vision Res.* 25: 1021–35
- Rolls, E. T., Judge, S. J., Sanghera, M. K. 1977. Activity of neurons in the inferotemporal cortex of the alert monkey. *Brain Res.* 130: 229–38
- Rolls, E. T. 1984. Neurons in the cortex of the temporal lobe and in the amygdala of

- the monkey with responses selective for faces. *Human Neurobiol.* 3: 209-22
- Saito, H., Yukie, M., Tanaka, K., Hikosaka, K., Fukada, Y., Iwai, E. 1986. Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *J. Neurosci.* 6: 145-57
- Sakata, H., Shibutani, H., Ito, Y., Tsurugai, K. 1986. Parietal cortical neurons responding to rotary movement of visual stimulus in space. *Exp. Brain Res.* 61: 658-63
- Sakata, H., Shibutani, H., Kawano, K. 1983. Functional properties of visual tracking neurons in posterior parietal association cortex of the monkey. *J. Neurophysiol.* 49: 1364-80
- Sakata, H., Shibutani, H., Kawano, K., Harrington, T. L. 1985. Neural mechanisms of space vision in the parietal association cortex of the monkey. *Vision Res.* 25: 453-63
- Schein, S. J., Desimone, R., deMonasterio, F. M. 1983. Spectral properties of V4 cells in macaque monkey. *Invest. Ophthalmol. Vis. Sci.* 24: 107
- Schein, S. J., Marrocco, R. T., deMonasterio, F. M. 1982. Is there a high concentration of color-selective cells in area V4 of monkey visual cortex? *J. Neurophysiol.* 47: 193-213
- Segraves, M. A., Deng, S.-Y., Bruce, C. J., Ungerleider, L. G., Mishkin, M., Goldberg, M. E. 1983. Monkeys with striate lesions have saccadic dysmetria to moving targets. *Invest. Ophthalmol. Vis. Sci.* 24: 25
- Seltzer, B., Pandya, D. N. 1984. Further observations on parieto-temporal connections in the rhesus monkey. *Exp. Brain Res.* 55: 301-12
- Shapley, R., Lennie, P. 1985. Spatial frequency analysis in the visual system. *Ann. Rev. Neurosci.* 8: 547-83
- Shipp, S., Zeki, S. 1985. Segregation of pathways leading from area V2 to areas V4 and V5 of macaque monkey visual cortex. *Nature* 315: 322-25
- Sterling, P., Wickelgren, B. G. 1969. Visual receptive fields in the superior colliculus of the cat. *J. Neurophysiol.* 32: 1-15
- Stone, J. 1983. *Parallel Processing in the Visual System*. New York: Plenum
- Symonds, L. L., Rosenquist, A. C. 1984. Laminar origins of visual corticocortical connections in the cat. *J. Comp. Neurol.* 229: 39-47
- Tanaka, K., Hikosaka, H., Saito, H., Yukie, Y., Fukada, Y., Iwai, E. 1986. Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *J. Neurosci.* 6: 134-44
- Tigges, J., Tigges, M. 1985. Subcortical sources of direct projections to visual cortex. See Peters & Jones 1985, 3: 351-78
- Tigges, J., Tigges, M., Perachio, A. A. 1977. Complementary laminar terminations of afferents to area 17 originating in area 18 and the lateral geniculate nucleus in squirrel monkey. *J. Comp. Neurol.* 176: 87-100
- Tigges, J., Tigges, M., Anschel, S., Cross, N. A., Letbetter, W. D., McBride, R. L. 1981. Areal and laminar distributions of neurons interconnecting the central visual cortical areas 17, 18, 19 and MT in the squirrel monkey (*Saimiri*). *J. Comp. Neurol.* 202: 539-60
- Tolhurst, D. J., Movshon, J. A. 1975. Spatial and temporal contrast sensitivity of striate cortex neurons. *Nature* 176: 87-100
- Tootell, R. B. H., Silverman, M. S., DeValois, R. L., Jacobs, G. H. 1983. Functional organization of the second cortical visual area in primates. *Science* 220: 737-39
- Tusa, R. J., Palmer, L. A., Rosenquist, A. C. 1981. Multiple cortical visual areas. See Woolsey 1981, 2: 1-32
- Ungerleider, L. G., Desimone, R. 1986. Cortical connections of visual area MT in the macaque. *J. Comp. Neurol.* 248: 190-222
- Ungerleider, L. G., Mishkin, M. 1982. Two cortical visual systems. See Ingle et al 1982, pp. 549-80
- Van Essen, D. C. 1979. Visual areas of the mammalian cerebral cortex. *Ann. Rev. Neurosci.* 2: 227-63
- Van Essen, D. C. 1985. Functional organization of primate visual cortex. See Peters & Jones 1985, 3: 259-329
- Van Essen, D. C., Maunsell, J. H. R. 1980. Two-dimensional maps of the cerebral cortex. *J. Comp. Neurol.* 191: 255-81
- Van Essen, D. C., Maunsell, J. H. R. 1983. Hierarchical organization and functional streams in the visual cortex. *Trends Neurosci.* 6: 370-75
- Van Essen, D. C., Maunsell, J. H. R., Bixby, J. L. 1981. The middle temporal visual area in the macaque: Myeloarchitecture, connections, functional properties and topographic representation. *J. Comp. Neurol.* 199: 293-326
- Van Essen, D. C., Zeki, S. M. 1978. The topographic organization of rhesus monkey prestriate cortex. *J. Physiol.* 277: 193-226
- von der Heydt, R., Peterhand, E., Baumgartner, G. 1984. Illusory contours and cortical neuron responses. *Science* 224: 1260-62
- von Grinau, M., Frost, B. J. 1983. Double-opponent-process mechanism underlying RF-structure of directionally specific cells

- of cat lateral suprasylvian visual area. *Exp. Brain Res.* 49: 84-92
- Wagor, E., Mangini, N. S., Pearlman, A. L. 1980. Retinal organization of striate and extrastriate visual cortex in the mouse. *J. Comp. Neurol.* 193: 187-202
- Weiskrantz, L., Saunders, R. C. 1984. Impairments of visual object transforms in monkeys. *Brain* 107: 1033-72
- Weller, R. E., Kaas, J. H. 1981. Cortical and subcortical connections of the visual cortex in primates. See Woolsey 1981, 2: 121-55
- Wild, H. M., Butler, S. R., Carden, D., Kulikowski, J. J. 1985. Primate cortical area V4 important for colour constancy but not wavelength discrimination. *Nature* 313: 133-35
- Wilson, M. 1978. Visual systems: Pulvinar-extrastriate cortex. *Handb. Behav. Neurobiol.* 1: 209-47
- Wilson, M., Wilson, W. A., Remez, R. 1977. Effects of prestriate, inferotemporal and superior temporal sulcus lesions on attention and gaze shifts in rhesus monkeys. *J. Comp. Physiol. Psychol.* 91: 1261-71
- Wilson, M., Keys, W., Johnston, T. D. 1979. Middle temporal cortical visual area and visuospatial function in *Galago senegalensis*. *J. Comp. Physiol. Psychol.* 93: 247-59
- Woolsey, C. N., ed. 1981. *Cortical Sensory Organization*. Clifton, NJ: Humana
- Wong-Riley, M. 1978. Reciprocal connections between striate and prestriate cortex in squirrel monkey as demonstrated by combined peroxidase histochemistry and autoradiography. *Brain Res.* 147: 159-64
- Wurtz, R. H., Goldberg, M. E., Robinson, D. L. 1980. Behavioral modulation of visual responses in the monkey: Stimulus selection for attention and movement. *Prog. Psychobiol. Physiol. Psychol.* 9: 43-83
- Wurtz, R. H., Mohler, C. W. 1976a. Enhancement of visual responses in monkey striate cortex and frontal eye fields. *J. Neurophysiol.* 39: 766-72
- Wurtz, R. H., Mohler, C. W. 1976b. Organization of monkey superior colliculus: Enhanced visual response of superficial layer cells. *J. Neurophysiol.* 39: 745-62
- Wurtz, R. H., Newsome, W. T. 1985. Divergent signals encoded by neurons in extrastriate areas MT and MST during smooth pursuit eye movements. *Soc. Neurosci. Abstr.* 11: 1246
- Wurtz, R. H., Richmond, B. J., Newsome, W. T. 1984. Modulation of cortical visual processing by attention, perception, and movement. See Edelman et al 1984, pp. 195-217
- Yin, T. C. T., Mountcastle, V. B. 1977. Visual input to the visuomotor mechanisms of the monkey's parietal lobe. *Science* 197: 1381-83
- Yin, T. C. T., Mountcastle, V. B. 1978. Mechanisms of neuronal integration in the parietal lobe for visual attention. *Fed. Proc.* 37: 2251-57
- Zeki, S. M. 1969. Representation of central visual fields in prestriate cortex of monkey. *Brain Res.* 14: 271-91
- Zeki, S. M. 1971. Cortical projections from two prestriate areas in the monkey. *Brain Res.* 34: 19-35
- Zeki, S. M. 1973. Colour coding in rhesus monkey prestriate cortex. *Brain Res.* 53: 422-27
- Zeki, S. M. 1974a. Cells responding to changing image size and disparity in the cortex of the rhesus monkey. *J. Physiol.* 242: 827-41
- Zeki, S. M. 1974b. Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *J. Physiol.* 236: 549-73
- Zeki, S. M. 1975. The functional organization of projections from striate to prestriate visual cortex in the rhesus monkey. *Cold Spring Harbor Symp. Quant. Biol.* 40: 591-600
- Zeki, S. M. 1977. Colour coding in the superior temporal sulcus of rhesus monkey visual cortex. *Proc. R. Soc. London Ser. B* 197: 195-223
- Zeki, S. M. 1978. Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *J. Physiol.* 277: 273-90
- Zeki, S. M. 1980. The representation of colours in the cerebral cortex. *Nature* 284: 412-18
- Zeki, S. M. 1983a. Colour coding in the cerebral cortex: The reaction of cells in monkey visual cortex to wavelengths and colours. *Neurosci.* 9: 741-65
- Zeki, S. M. 1983b. Colour coding in the cerebral cortex: The responses of wavelength-selective and colour-coded cells in monkey visual cortex to changes in wavelength composition. *Neurosci.* 9: 767-81
- Zeki, S. M. 1983c. The distribution of wavelength and orientation selective cells in different areas of monkey visual cortex. *Proc. R. Soc. London Ser. B* 217: 449-70
- Zihl, J., von Cramon, D., Mai, N. 1983. Selective disturbance of movement vision after bilateral brain damage. *Brain* 106: 313-40