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CHAPTER 6

Visual Information Processing in the Primate Brain

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INTRODUCTION

The visual system is the most widely studied and perhaps the best understood mammalian sensory system. Not only have the details of its anatomical features been well described, but the behavior of its neurons have also been characterized at many stages of the neural pathway. For this reason, the visual system has also become the system of choice for the study of both sensory coding as well as for such higher cognitive processes as memory and attention. In this chapter we will focus on the visual system of non-human primates, since in the past 10-15 years it has been extensively studied and because they provide an excellent animal model for understanding human vision.

THE RETINA

Our visual world is complex and dynamic. To successfully interpret this world the visual system performs the analysis of various attributes of the visual

image and then integrates these attributes into a percept of a visual scene. The most fundamental characteristic

of our visual world is that it is not uniform in time and space, and the visual system is well designed to analyze these non-uniformities. Such fundamental dimensions of visual stimuli as spatial and temporal variations in luminance and chromaticity are encoded at the level of the retina, while the encoding of other more complex stimulus features, such as motion, complex form and depth, emerge at the level of visual cortex.

The Retinal Image

The retina is the sheet of neural tissue, some 0.3-0.4 mm thick (300-400 μm) and about 520 mm^2 in area, that lines the back portion of the eye where the image of light rays focused through the cornea and lens is formed. Since the eye is first and foremost an optical system, this image on the retina is measured in terms of visual angle, which is the angle formed by rays

emanating from an object to their point of focus near the back surface of the lens (the so-called “nodal Rays diverging from the nodal point form the same angle as they impinge on the retina. Thus, the length and height of the retinal image formed by objects of different size and distance in the physical world will be the same if the visual angles formed by those objects are the same. These dimensions depend critically on the size of the eye. The macaque eye is roughly 67% the size of the human eye, and the distance on the retina that corresponds to one degree of visual angle is therefore about 67% that for the human retina, 200 μm vs. 290 μm (Drasdo and Fowler, 1974). Thus, how far eccentric an object on the retina is from the point of central fixation can be described using this simple conversion either by the angle in visual degrees that object makes with the fixation point or by its distance from this point in μm (or mm). The point of central fixation on the retina corresponds to the fovea, an area about 1.5 mm (or 7 deg) in diameter specialized for the best possible optical path and high acuity (discussed below). Eccentricity on the retina is therefore measured with respect to the center point of the fovea. The conversion between linear distance and visual angle depends somewhat on eccentricity due to changes in the eye’s optics, especially for eccentricities greater than 50 deg or so (Drasdo and Fowler, 1974).

Retinal Design

Because of its location in the eye, the retina is often misconstrued as a peripheral structure, more a part of the eye than of the brain. In fact, the retina is an extension of the central nervous system, much like the olfactory bulb. Like the rest of the brain, the retina comprises a great diversity of neuronal cell types, some 60-70 distributed across five classes of neuron within six primary layers (Figure 6.1). A tremendous degree of specialization for functional circuitry is therefore obtained by permuting these types in different combinations (reviewed in Masland & Raviola, 2000).

The basic architecture of the vertebrate retina includes an array of *photoreceptors* (the input element) that transduce absorbed light into electrical activity and an array of *ganglion cells* that encode this activity as a train of action potentials carried along axonal fibers of the optic nerve. The macaque retina contains about 50 million photoreceptors that converge through layers of retinal circuitry upon some 1.5 million ganglion cells (Rodieck, 1988; Curcio et al., 1989). The output of the photoreceptor mosaic is carried to the ganglion cells via parallel and iterative circuits composed of serial connections between a variety of both excitatory and inhibitory inter-neurons (Figure 6.2). The activity of a ganglion cell at a particular moment in its physiological history is therefore the confluence of all excitation and inhibition in its pre-synaptic circuitry.

point”; see Rodieck, 1998 or Wandell, 1995).

Excitation in and from the retina is conveyed primarily through the feed-forward circuit from photoreceptors

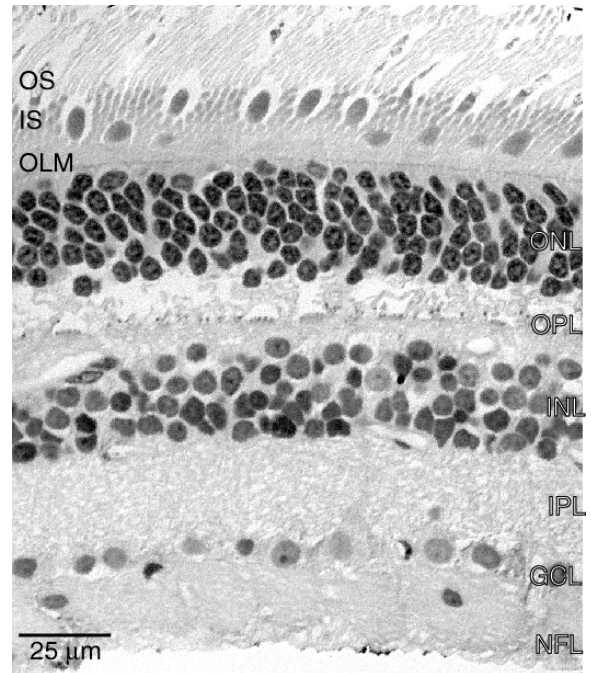


Figure 6.1. Photomicrograph of radial section through macaque retina (*macaca fascicularis*) demonstrating major cellular layers and structures. The thin, pigment-containing outer segment (OS) and thicker, light-funneling inner segment (IS) of each photoreceptor is separated from the cell body by the outer limiting membrane (OLM), which stabilizes the photoreceptor layer as it penetrates the retinal pigment epithelium (not shown). The outer (closest to the brain) and inner (closest to the lens of the eye) retina are each comprised of a *nuclear* layer, containing cell bodies, and a *plexiform* layer, containing intermingled axons and dendrites of cells forming synaptic contacts with one another. The outer nuclear layer (ONL) contains the cell bodies of the photoreceptors, which send their axon terminals to the outer plexiform layer (OPL) to contact the post-synaptic processes of bipolar and horizontal cells. The inner nuclear layer (INL) contains the cell bodies of horizontal cells, closest to the OPL, and the cell bodies of bipolar and amacrine cells, which send their axonal processes to the inner plexiform layer (IPL) where they contact one another and the dendrites of ganglion cells. The ganglion cell layer (GCL) contains the cell bodies of the ganglion cells (and some displaced amacrine cells), while the nerve fiber layer (NFL) contains the axons of the ganglion cells on their way to the optic nerve.

to ganglion cells via a class of intermediate neurons called *bipolar cells*. In mammalian retina, this circuit is entirely *glutamatergic* – each element transmits information from its axon terminal to the next level of processing by the release of glutamate (Massey, 1990). Inhibition within the retina, in contrast, is conveyed primarily through two levels of feedback circuits. In the outer retina, *horizontal cells* collect excitation from a large number of photoreceptors (discussed below) and provide inhibition proportionally back to the

photoreceptors themselves and to the dendritic trees of bipolar cells (Dacey et al., 2000).

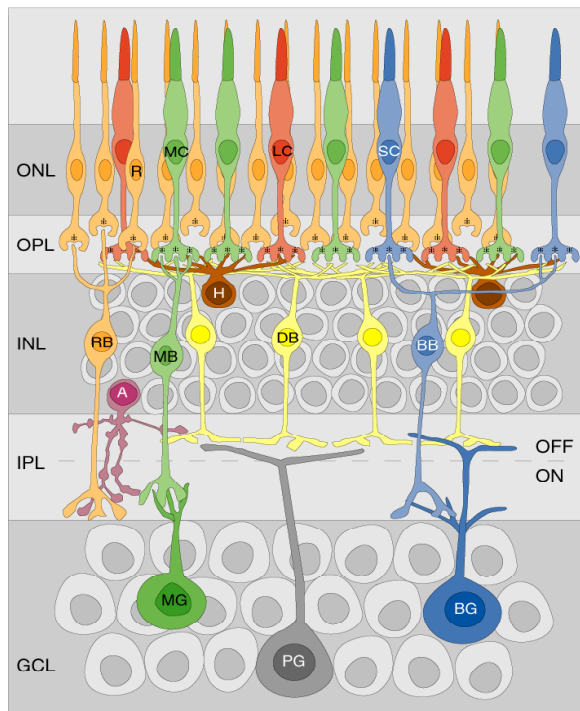


Figure 6. 2. Schematic diagram of macaque retina indicating major cell types and their circuits. Each photoreceptor synapse is marked by a dense synaptic “ribbon” that facilitates the release of glutamate from the axon terminal. Rod photoreceptors (R) send their signals to a specialized amacrine cell (A) via a single type of rod bipolar cell (RB). Middle-wavelength sensitive cones (MC) and long-wavelength sensitive cones (LC) both contact midget ganglion cells (MG) via a narrow-field midget bipolar cell (MB) and parasol ganglion cells (PG) via large-field diffuse bipolar cells (DB). Short-wavelength cones (SC) send signals for blue color vision to a specialized bistratified ganglion cell (BG) via the so-called “blue cone” bipolar cell (BB). Inhibitory horizontal cells (H) collect signals from photoreceptors over a large area and make feed-back contacts both to the photoreceptors and to the bipolar cells. The IPL is subdivided into an OFF region, for contacts between cells used in signaling light decrements from the mean, and an ON region, for contacts between cells used in signaling light increments from the mean. Other abbreviations as in Figure 6.1.

This inhibition modulates the release of glutamate by the photoreceptor and its excitatory effect on bipolar cells. In the inner retina, *amacrine cells* collect more localized excitation from bipolar cells and provide inhibition back to the bipolar cell axon and to the dendritic trees of ganglion cells (Sterling, 1998). The role of inhibition in the retina is therefore to modulate the degree of excitation both at the release sites for glutamate and at its post-synaptic targets.

Certain fundamental properties of retinal cell populations have bearing on the organization of higher levels of visual processing. Cells within a type form a

continuous mosaic that determines the spacing between cells and their sampling density (typically expressed as cells mm^{-2} or as cells deg^{-2}) as a function of eccentricity. With increasing eccentricity, the density of the mosaics for most retinal neurons decreases (with some notable exceptions), as the spacing between neurons increases. For example, ganglion cell density peaks in the fovea at about 60,000 cells mm^{-2} and falls to 10,000 cells mm^{-2} at 20 deg and to 1000 cells mm^{-2} at 40 deg (Wassle et al., 1990). Cells within a particular mosaic cover the retina so that signals from each location in the photoreceptor mosaic are represented at least once within that mosaic. This implies that as the density of a particular cell type decreases with increasing eccentricity, the area covered by that cell’s processes (the so-called “collecting aperture”) becomes larger to accommodate the greater spacing between photoreceptors. For example, as the density of horizontal cells decreases from 20,000 cells mm^{-2} in the fovea to 2000 cells mm^{-2} at 30 deg eccentricity, the area of the photoreceptor mosaic from which their processes collect increases by a factor of 25 (Wassle et al., 1989). Generally, the anatomical area covered by an individual retinal neuron increases at a rate greater than the rate of decrease in density of any retinal mosaic. This implies that the convergence of pre-synaptic neurons to a particular cell increases with increasing eccentricity (Calkins and Sterling, 1999). Consequently, in moving from the fovea to the periphery, both the spatial tuning of any single retinal neuron and the spatial resolution of that neuron’s mosaic decrease dramatically. From a functional perspective, this natural property of retinal cell types establishes the first limit for the well-known decrease in spatial resolution for psychophysical channels with increasing retinal eccentricity.

Retinal Cell Types

Each of the five classes of neurons in the retina is specialized for a broad function in encoding visual information, loosely delineated between excitation and inhibition. However, our visual world contains a diverse spectrum of spatial, temporal and spectral variations, spanning a large range of contrasts and frequencies. The most efficient means to encode such diverse information with the highest possible fidelity is to partition the task among different circuits, each specialized for serving a particular portion of the visual dynamic range (Sterling, 1998). To accommodate this need for specialization, each class of retinal neuron is comprised of several cell types, each type demonstrating a unique combination of morphology, connectivity, neurochemistry and physiology (Masland and Raviola, 2000). It is the precise connectivity between different types that render each retinal circuit

uniquely tuned to different aspects of visual information.

Photoreceptors

About 94% of the photoreceptors are rods, each sufficiently sensitive to signal the absorption of even a single photon at the absolute threshold of vision. Rods dominate the photoreceptor population over most of the retina, with a peak density of 170,000 rods mm⁻² at 15 deg eccentricity, which drops to 50,000 – 70,000 rods mm⁻² at 45 deg. The fovea contains a small region, about 150 µm in diameter, that is rod-free, completely avascular and devoid of all post-photoreceptor elements of the retina, which are displaced laterally to form the foveal wall. This region contains the highest density of cone photoreceptors, which comprise the remaining 6% and are each capable of operating at light levels eliciting as many as 10 million photon absorptions per cone each second. The cone density peaks at about 210,000 cones mm⁻² and drops precipitously to about 5000 cones mm⁻² at 20 deg (Curcio et al., 1989; Wässle et al., 1990). For both rods and cones, the light-funneling inner segment of the photoreceptor increases in diameter the further it is from fovea, with a 5-fold increase for cones and a 3-fold increase for rods. Thus, the collecting aperture of each photoreceptor increases with eccentricity, as it does for other retinal neurons.

Light funneled through the photoreceptor inner segment enters the outer segment where, if it is absorbed by the light-sensitive photopigment, it elicits a biochemical cascade called “phototransduction”. The two classes of photoreceptors, *rods* and *cones*, show both similarities and differences in their response to light. In the dark, rods and cones are relatively depolarized to a resting potential of about -40 mV due to the net influx of positive ions through cyclic-G-gated channels in the outer segment (for review, see chapter six in Rodieck, 1998). When photons are absorbed, a G-protein coupled cascade is initiated which ultimately results in the closure of these ion channels, thus hyperpolarizing the photoreceptor. Despite these similarities, there are notable differences between this cascade for rods and cones that render several distinctions in their physiological responses to light. Key among these differences is the more rapid activity of an enzyme in the outer segment of the cone to maintain a steady concentration of cyclic-G. This enhanced activity is likely to underlie the faster response of the cone to light, and its faster recovery. Thus, the pathways collecting signals from cones will be faster than those collecting from rods. Furthermore, unlike rods, cones will not saturate in bright lights and demonstrate different rates of adaptation to light (for review, see Baylor, Nunn, & Schnapf, 1987).

The proportion of cyclic-G-gated channels that close for a particular photoreceptor and the amplitude of this hyperpolarization depends upon the rate of photon absorption. The number of photons funneled through the inner segment and their wavelength determines this rate. Therefore the key variable in phototransduction is the spectral sensitivity of the photopigment. Rods all contain a single photopigment, called rhodopsin, with a peak sensitivity near 500 nm. Cones, on the other hand, distribute into three types defined by differences in the photopigments they express. Short (S) wavelength sensitive cones contain a pigment that peaks in sensitivity around 430 nm, near the region of the spectrum where we perceive violet and blue. These cones comprise on average only about 5% of all cones (reviewed in Calkins, 2001). Middle (M) wavelength sensitive cones contain a pigment that peaks at 535 nm, near where we perceive green, and long (L) wavelength sensitive cones contain a pigment peaks at 567 nm, near where we perceive orange (Baylor et al., 1987). Together, M and L cones comprise the remaining fraction of cones and in macaque retina are present in about equal numbers (Packer et al., 1996).

The expression of different types of cone in the photoreceptor mosaic allows primates to discriminate surfaces based on differences in spectral reflectance. The difference between signals from M and L cones is fed to a mechanism underlying discrimination between red and green (red/green), while the difference between S cones and the summed signal from M and L cones is fed to a mechanism providing the basis for discriminating blue from yellow (blue/yellow). The combined activity within the red/green and the blue/yellow channels ultimately provides the wide range of colors we experience (Wandell, 1995).

Horizontal Cells

In the dark, the relative depolarization of the photoreceptor – like depolarization in other neurons – promotes an influx of Ca²⁺ ions into the axon terminal and a release of glutamate from the photoreceptor synapse. Retinal neurons, with the exception of ganglion cells, are unmyelinated and do not produce action potentials. Instead, voltage fluctuations are conveyed through the electrotonic spread of ions in grades of current flow. Thus, the release of glutamate from the photoreceptor synapse is correspondingly graded from its highest release rate in the dark to lower rates with increasing light absorption and hyperpolarization of the photoreceptor. Each cone photoreceptor is coupled electrically to its neighbors and to neighboring rods via small junctions of shared membrane of the axon terminal called “gap junctions” (Tsukamoto et al., 1992). These junctions are

essentially electrical resistors, and are thought to allow a limited degree of spread of current from one cone to another or from cone to rod (and *vice versa*). Gap junctions likely serve to average or electrotonically smooth the conjoint activity of the photoreceptor mosaic (Sterling, 1998). Therefore the release of glutamate from a photoreceptor reflects mostly the rate of light absorption within its own outer segment, but also to a lesser extent the level of light activity in its neighbors.

Closest to the point of glutamate release from the photoreceptor synapse are the processes of horizontal cells (Figure 6.2), which are thought to collect excitation from the synapse and provide inhibitory (GABAergic) feed-back to the photoreceptor axon terminal (Vardi et al., 1992; Vardi et al., 1994; Sterling et al., 1995). This feedback is thought to drive the photoreceptor membrane potential towards its resting or “dark” value, thereby reducing the release of glutamate (Kamermans and Spekreijse, 1999). There are two types of horizontal cells in the primate retina (Wassle and Boycott, 1991). The H1 cell has one arbor that collects from (and feeds back to) M and L cones, but not S cones, and a second arbor that is separated from the main arbor by a long axon-like process that contacts rods. The HII cell has a main arbor and a smaller arbor that both collect from all cone types, but not from rods. Therefore the spectral sensitivity of both H1 and HII cells is broadband (Dacey, 2000). Each horizontal cell collects from multiple photoreceptors. For example, the H1 cell collects from some 15-25 cones in the fovea and from 10-15 further in the periphery as the spacing between cones increases (calculated from Wassle et al., 1989). However, H1 cells couple electrotonically to one another via gap junctions, and HII cells are likewise interconnected. This connectivity produces a large network of horizontal cells that effectively enlarges laterally the photoreceptor input to any one cell. Consequently, the feedback to any single photoreceptor reflects not only its own activity, but the average activity pooled across two independent networks of horizontal cells. Because of the inter-cell coupling between horizontal cells, the feedback is not only spatially, but also temporally low-pass: the inhibition is broad and slow (Smith et al., 2001).

Bipolar Cells

The release of glutamate at the photoreceptor axon terminal fluctuates up and down from some baseline rate set by the average activity in the outer retina (for review, see Rodieck, 1998). These fluctuations constitute information, so ultimately both directions of change in glutamate release need to be encoded as excitation at the photoreceptor to bipolar cell synapse.

Roughly half of the 10-12 types of bipolar cell respond with excitation (depolarization) to increments in local light activity (“ON cells”), while the remainder responds to decrements in activity (“OFF” cells) (Boycott and Hopkins, 1991). This division of labor is accomplished by a simple molecular trick at the bipolar cell dendritic tree. ON bipolar cells express *metabotropic* glutamate receptors that gate cation channels with decreasing glutamate (i.e., increasing light), while OFF bipolar cells express *ionotropic* receptors that gate cation channels with increasing glutamate (decreasing light) (Morigiwa and Vardi, 1999). In this way, only a single neurotransmitter (glutamate) is required to encode both increments and decrements from the average photoreceptor activity. The physiological division into ON and OFF also correlates with a morphological division. ON bipolar cells send long axons into the proximal half of the inner plexiform layer, closest to the ganglion cell layer, while OFF bipolar cells have shorter axons that stratify in the distal half of the inner plexiform layer (Boycott and Hopkins, 1991) (Figure 6.2).

Rod bipolar cells. Each rod diverges to 2-3 representatives of a single type of ON bipolar cell. Each of these so-called “rod” bipolar cells collects signals from 12-15 rods in the central retina, increasing gradually to 50-60 rods in the periphery (Grunert and Martin, 1991). At night, both the absolute level of light and the contrast from a reflective surface are far less. Thus, the retinal circuit for rod or *scotopic* vision, like the rod itself, is designed to transmit with the highest possible sensitivity. The convergence of so many rods to the rod bipolar cell increases this sensitivity, so that the signal from the absorption of even a single photon of light is preserved and transmitted with great fidelity (Makous, 1990). Interestingly, the collected excitatory signal from this pool of rods is conveyed indirectly to different types of ganglion cells via a specialized amacrine cell (the AII amacrine) that contacts both ON and OFF bipolar cells (Strettoi et al., 1990). The functional significance of this divergence is not known, but it probably serves to send copies of the signal from rare photon events in the dark to the multiple types of ganglion cells.

Cone bipolar cells. Cones diverge to the remaining 9-11 types of bipolar cell. Each of these types has a unique expression of particular subunits of glutamate receptor (DeVries, 2000). This pattern bestows upon each type a unique physiology that in turn contributes to the particular spectral, spatial and temporal properties of the ganglion cells to which they connect. To a first approximation, for a particular ON type there is an analogous OFF type bipolar cell type. Since in the mammalian retina bipolar cells are likely to only use glutamate as their neurotransmitter (Massey, 1990),

their response polarity (ON or OFF) is conserved in the synapse to the ganglion cell. Thus, some 85-90% of the ganglion cells are either ON or OFF, while the rest are both (Watanabe and Rodieck, 1989; Dacey and Lee, 1994a). Most morphological types of ganglion cells therefore also distribute into separate ON and OFF mosaics that respond, respectively, to light increments or light decrements (Famiglietti and Kolb, 1976). Cone bipolar cells distribute into two main categories, *midget* and *diffuse*, defined by differences in the morphology of their dendritic trees and the number of cones contacting them (for review see Boycott & Hopkins, 1997). These subsystems have distinct roles in early visual processing.

The primate retina is highly specialized for supporting the highest possible spatial acuity. In the fovea, discrimination of spatial patterns is limited in resolution only by the spacing of the cone photoreceptors (Williams, 1986). This corresponds to about 40 cycles deg^{-1} spatially in the macaque monkey retina and at 60 cycles deg^{-1} in the human retina (Samy and Hirsch, 1989). To support this acuity, each cone contacts a single ON and a single OFF *midget bipolar cell* and, over most of the retina, each midget cell collects from only a single cone (Calkins and Sterling, 1999) (Figure 6.2). Far in the periphery, beyond about 45 deg, up to 3-5 cones may contact each midget bipolar cell (Wassle et al., 1994). In contrast, each of the six or so types of diffuse bipolar cells collect from 8-12 cones over the entire retina with types named DB1-DB3 providing OFF signals to the inner retina and the types named DB4-DB6 providing ON signals (Boycott and Hopkins, 1991). We know very little about the separate mosaics and physiology of these diffuse cells. But, with so many cones converging on each, the diffuse system appears to have sacrificed spatial resolution for higher contrast sensitivity, and with higher sensitivity comes a sharper temporal response (DeVries, 2000). These differences between the midget and diffuse bipolar cells are apparent in the responses of ganglion cells to which they provide input (see below). Thus, the first segregation of functional pathways in vision occurs where the cone synapse diverges to different types of bipolar cell

Ganglion Cells.

Receptive Fields. The response of a particular retinal neuron to a given pattern of light impinging on the photoreceptor array depends on the distribution of spectral, spatial and temporal energy within that pattern. The quality and degree of tuning to this energy depends upon the structure of the *receptive field* of the neuron consisting of an excitatory *center* arising from the photoreceptor \rightarrow bipolar cell \rightarrow ganglion cell circuitry and an inhibitory *surround* arising from the

lateral circuitry of horizontal and amacrine cells (reviewed in Sterling, 1998). A neuron responds therefore with increased activity to an appropriate stimulus imaged upon its receptive field center and with decreased activity when that same stimulus is imaged upon the surround.

The precise physiology of the center and surround for a particular retinal neuron depends on the circuitry providing its pre-synaptic input and where that neuron is in the retinal hierarchy. For example, the center of the receptive field of a photoreceptor is formed primarily by that photoreceptor, plus the excitation pooled from its neighbors via gap junctions (Smith and Sterling, 1990). On the other hand, the center for a bipolar cell is comprised of the contributions from overlying photoreceptors (Dacey et al. 2000). Similarly, the excitatory center of a ganglion cell arises from the convergence within the photoreceptor to the bipolar cell circuitry that contacts its dendritic tree, while much (but likely not all) of the inhibitory surround arises in the lateral connections from horizontal cells to photoreceptors (and bipolar cell dendrites) (Freed et al., 1992; Vardi et al., 1994). Thus, spatially the center and surround are quantified in reference to the area of the photoreceptor mosaic contributing to each.

The response amplitudes of the center and surround are spatially non-uniform, each is roughly Gaussian in shape and depends upon the spatial distribution of the synaptic contributions from the cells contributing to each (Croner & Kaplan, 1995). Also, because of anatomical and physiological differences between the cells that comprise them, the center of the receptive field is spatially narrower, temporally quicker, and spectrally sharper (i.e., more wavelength dependent) than is the surround (Dacey and Lee, 1994b). The center also tends to be greater in amplitude than the surround, generally by 35-40% for ganglion cells (Croner & Kaplan, 1995), and thus, when a stimulus fills the entire receptive field, the center response dominates. In this sense, the surround can be considered as a spatial and temporal filter for subtracting the redundancy that inevitably is present in a typical natural scene, while the center conveys the signal for whatever spatial and temporal contrast remains. In other words, the surround essentially filters the background activity, and what is transmitted at the photoreceptor axon is the contrast or “edge” provided by modulation of light activity above or below this background.

Because each retinal neuron derives its input from overlying photoreceptors, most often the receptive field is quantified spatially with reference to the region of the photoreceptor mosaic that elicits a modulation of the cell’s activity. However, since stimuli are multi-dimensional, it is equally important to understand the spectral and temporal characteristics of the receptive

field. Because receptive fields of retinal neurons are tuned to different types of information receptive field function as a *filter*, passing certain bandwidths of information while filtering out others. For example, the horizontal cell contribution to the surround is often referred to as a *low-pass* spatiotemporal filter, since it is broad spatially and slow temporally and therefore tuned to low spatial and temporal signals (Srinivasan et al., 1982).

Ganglion Cell Mosaics. Even though the fovea only comprises 1-2% of the retinal surface area, it contains more than 35% of all retinal ganglion cells (calculated from Wassle et al., 1989). Though the peak density of ganglion cells (about 60,000 cells mm⁻²) is less than the peak cone density by more than a factor of three, the tight packing of cells within the fovea renders the effective sampling of the ganglion cell mosaic much higher, with 3-4 ganglion cells per cone (Wassle et al., 1989). This is sufficient to provide each cone access to several parallel ganglion cell circuits serving different visual functions and explains, at least in part, the expansion of the foveal representation in V1 (see below). The functionality of these circuits correlates strongly with ganglion cell morphology, which in turn reflects the nature of its pre-synaptic inputs. The number of these types depends critically upon species. For the primate retina, the number is likely 15-20, each with a distinct pattern of pre-synaptic input, physiology, and central projection into the thalamus (Leventhal et al., 1981; Rodieck and Watanabe, 1993). The circuits for most of these and their role in visual information processing are unknown. Nevertheless, there are a few circuits in the primate retina about whose function we can say a great deal, though it is probably imprudent to call them “solved”. These divide broadly first into ON and OFF, following the pairing of ON and OFF bipolar cell types, and this is reflected by the level of stratification of the ganglion cell dendritic tree in the inner retina (Figure 6.2; Dacey & Lee, 1994a). These circuits also divide broadly according to whether the bipolar cell input is midget or diffuse, for this will determine the spatio-temporal and spectral responses of the ganglion cell.

What the cortex ultimately reads as retinal output are spectral, spatial and temporal signals filtered through the receptive fields of individual ganglion cells. Since the filter properties of ganglion cells are determined by their pre-synaptic circuitry, this circuitry determines what specific types of visual information is filtered at the first stage of visual processing.

Midget or “P” Ganglion Cells. Midget bipolar cells collect from a single cone over most of the retina and each cone diverges to a single ON and single OFF midget bipolar cell (Wassle et al., 1994). In and around

the fovea, each ON and OFF midget bipolar cell contacts a single ON or OFF midget ganglion cell, and no midget ganglion cell collects from more than one midget bipolar cell (Calkins and Sterling, 1999). In this way, the greatest possible spatial resolution – that of a single cone – is afforded to the receptive field center of the midget pathway, for both light increments and decrements. Midget ganglion cells comprise about 80% of the ganglion cells in the foveal region (Perry et al., 1984), so the expansion of the foveal representation in V1 is in large part due to the presence of the midget system (Wassle et al., 1989). Outside of the fovea, as the optics of the eye worsens and the spacing between cones increases (Hirsch, 1984), the dendritic tree of the midget ganglion cell expands considerably, and each cell collects from increasing numbers of midget bipolar cells and cones (Calkins and Sterling, 1999). Even so, these ganglion cells remain the smallest and most numerous, with the least convergence of cones.

Midget ganglion cells provide the dominant retinal input to the parvocellular region of the lateral geniculate nucleus (LGN, see below). For this reason, midget cells are often referred to as “P” cells, as are the parvocellular relay neurons to which they connect. For the most part, the physiological properties of P cells in the LGN mimic those of the midget/P cell in the retina. Thus, the LGN P cell also demonstrates a small receptive field center that corresponds to the small dendritic tree of the midget ganglion cell. In fact, despite inevitable variation between different sets of experiments, the physiological measurements of the spatial extent of the P cell center match very well the anatomical convergence of cones to the midget ganglion cell across retinal eccentricities (Figure 6.3). Thus, for this circuit, the anatomy reasonably predicts the spatial properties of the receptive field center.

Over the entire retina, the receptive field center of the midget/P cell is the most narrow of all ganglion cell receptive fields and the sampling density of the midget cell mosaic establishes the limit of spatial acuity (Croner & Kaplan, 1995; Dacey, 1993). However, since the convergence of cones to the midget cells is minimal, its spatial contrast sensitivity is relatively poor (Croner & Kaplan, 1995). For reasons we do not yet understand, but no doubt arising in part from the small number of cones converging upon it, the midget ganglion cell is also temporally sluggish and responds to light in a sustained fashion. Thus, the spatio-temporal contrast sensitivity of the midget cell is distributed across high spatial, but lower temporal frequencies (see Figure 6.5 for the equivalent properties in the LGN).

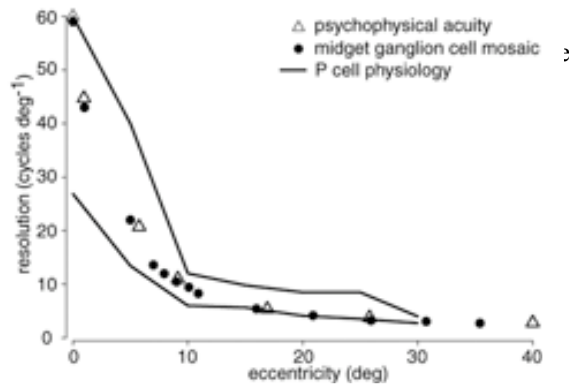


Figure 6.3. Spatial resolution of the high acuity system. The high frequency cutoff for spatial resolution in cycles deg^{-1} is plotted against retinal eccentricity for three independent measures. Psychophysical acuity for human observers (triangles) is replotted from Anderson et al. (1991) who used the drifting grating protocol to measure the upper limit of spatial resolution. Acuity for the center fovea was adopted from Williams (1986). Resolution of the midjet ganglion cell mosaic in human retina (circles) was measured using inter-cell spacing and replotted from Dacey (1993). Resolution of physiological measurements from P cells in macaque retina and LGN (lines) was calculated from the diameter of the P cell receptive field center. Cell density was estimated from the diameter assuming a coverage factor of unity (Watanabe and Rodieck, 1989), and resolution calculated as the Nyquist limit assuming triangular packing (Williams, 1986). A range of physiological measurements of macaque P cell receptive field centers in retina and LGN was used to calculate lower and upper bounds (Derrington & Lennie, 1984).

The mosaic of M and L cones in the primate retina is patchy, with cones of like type distributing into small clusters. Because each midjet ganglion cell collects from only a single cone in and near the fovea, their excitatory connections are by definition finely tuned spectrally, conferring upon the midjet cell high *chromatic contrast sensitivity*. As the number of cones increases, some cells remain finely tuned to M and L cone modulation (Martin et al., 2001), while others begin to respond preferentially to luminance (M+L) modulation. Whether the cortex uses whatever chromatic sensitivity is present in the midjet mosaic as the basis for red/green color discrimination across the retina is a matter of debate (Calkins and Sterling, 1999). What is undeniable is that midjet cells, because of their fine spatial apertures (see above), are highly specialized and likely evolved primarily as a system to support foveal acuity limited only by the spacing of the cones.

Parasol or “M” Ganglion Cells Like the midjet ganglion cell, the *parasol* ganglion cell comes in both ON and OFF types, both of which have a broad,

circularly symmetric dendritic tree that resembles a parasol one might carry to keep the rain off. At a given retinal eccentricity, the area covered by the dendritic tree of the parasol cell is some 20 times the area covered by a midjet cell (Watanabe and Rodieck, 1989), and the parasol mosaic is accordingly sparser, comprising some 5-8% of all ganglion cells (Grunert et al., 1993). As a consequence of its size, the convergence of cones to the parasol cell is also a factor of 20 greater. For example, in the fovea, the parasol cell collects from 20-25 cones via 4-5 diffuse bipolar cells (Calkins, 1999). Physiologically, this contributes to a broader receptive field center with higher contrast sensitivity, about six times greater on average than that of the midjet ganglion cell (Croner & Kaplan, 1995). It is likely that the nature of its bipolar cell input, diffuse vs. midjet, also contributes to its characteristic transient response to light – the response fades for stationary stimuli and is optimal for stimuli moving across the photoreceptor mosaic (Kaplan and Shapley, 1986; Kaplan et al., 1988; Kaplan et al., 1990). Thus, the parasol cell responds best to lower spatial frequencies, higher temporal frequencies and to differences in retinal luminance. In terms of their projections to the brain, parasol ganglion cells provide the dominant retinal input to the magnocellular region of the LGN (Perry et al., 1984). Thus, they are generally called “M” cells. Like their retinal counterparts, M cells in the LGN have a receptive field center that is much broader than that of P cells, corresponding to the larger dendritic tree of the parasol ganglion cell. There is also some evidence that some parasol cells may send axon collaterals to the superior colliculus (for review, see Rodieck & Watanabe, 1993).

The retinal image is constantly in motion, due to small eye movements (for review, see Rodieck, 1998). Superposed upon this inherent movement is the actual translation of objects in a natural scene, or stimulus motion. This movement of stimuli across the photoreceptor mosaic at once blurs the spatial information contained in those stimuli, while introducing light contrast at higher temporal frequencies. Some mammalian retinas (e.g. rabbit retina, see Vaney, 1994; Vaney, Peichl, & Boycott, 1981) have ganglion cells tuned to specific directions of moving stimuli. The primate retina, to our knowledge, does not have this type of directional selectivity. However, what ultimately becomes a motion signal higher in the cortical streams is likely to originate at least in part from the transient responses propagating through the mosaic of the parasol cells as a stimulus moves across the photoreceptor array.

Other Ganglion Cells and Their Circuit The primary ganglion cell input to the LGN, in terms of numbers of cells, is provided jointly by the midget (P) and parasol (M) mosaics (Perry et al., 1984). Nevertheless, it is incorrect to associate only retinal midget cells with the parvocellular LGN and only parasol cells with the magnocellular LGN. Despite the convenience of this simplification, it remains just that - a simplification. Retrograde labeling of ganglion cells following injections of markers into the LGN reveal a diverse array of more sparsely populating ganglion cells, each with a unique morphology and, presumably, retinal circuitry (Rodieck and Watanabe, 1993). Though we know little about the function of these cells, we now appreciate that some of them are likely to project not to the primary P and M layers of the LGN, but to the intercalated or koniocellular layers in between (discussed below). One of these is the small bistratified ganglion cell that is implicated in color vision used to discriminate blues from yellows. The receptive field of this cell is such that signals from S cones oppose those from M and L cones in an antagonistic fashion. This antagonism is spatially overlapping, so the small bistratified cell is tuned sharply to spectral (chromatic) differences and very little to spatial edges (Dacey, 1996; Calkins et al., 1998).

What the Retina Responds To

In laying out a basic understanding of the retina it is important to point out that there is a difference between a perceptual attribute and the physical stimulus that elicited it. For the latter has very much to do with the retina, which interfaces the brain with the external visual world, while the former is something more ambiguous, ascribed to the stimulus by a host of (we presume) physiological interactions working in concert through higher visual areas of the brain. The former has to fit into our internal representation of the visual world that is built upon an earlier, more rudimentary representation in the output of the retina. For example, color is an attribute of the internal representation of a surface that arises from the retinal representation of the spectral reflectance of that surface. Similarly, motion is an attribute our internal representation provides for the displacement of an object in space and time that arises from local differences in the activity of ganglion cells as the image of that object steps across the retinal array. Motion is, in simple terms, something that is computed by the cortex based on changes in retinal firing patterns in response to the changing image upon the photoreceptor array. Certain ganglion cells in the primate retina may indeed respond favorably to a moving stimulus, but this does not imply that motion is encoded within the retina - the stage for what will

become the perception of motion is merely set in the retina. Other cells will respond to a stimulus that, to the human observer, appears colored, but color is not itself assigned by retinal activity. Thus, the complexity of the retinal wiring has less to do with perception and more to do with encoding the critical events that the cortex interprets as vision.

It is also critical to emphasize that while each of the circuits shown in Figure 6.2 underlies tuning of ganglion cell receptive fields for particular spatial, temporal or spectral frequencies, most types of ganglion cells respond in some measure to more than one attribute of a visual stimulus. For example, a midget ganglion cell will respond to a light moving across its receptive field, providing that movement is within the temporal sensitivity profile of the receptive field (see Figure 5A and B). Also, a parasol cell will respond to a fine spatial pattern, even though its broad receptive field is not necessarily specialized to convey the highest frequencies within that pattern. The point is that what we ultimately experience as vision arises from the confluence of activity across the mosaic of each type of ganglion cell, and rarely is any one type completely silent in that mass contribution.

Parallel Visual Pathways from the Retina

Visual pathways comprise a massive sensory component that involves about 90% of the retinal ganglion cells, those that project to the lateral geniculate nucleus (LGN) of the thalamus and from there to the primary visual cortex (figure 6.4) (Hendrickson et al., 1978; Rodieck & Watanabe, 1993).

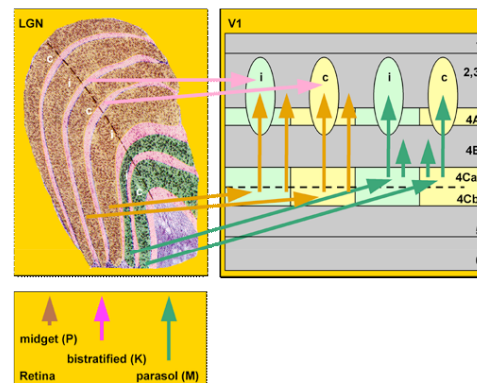


Figure 6.4. Schematic of early visual pathways from retina to V1. In retina, three main types of ganglion cell project to the P, M and K regions in the LGN. The six primary M and P layer of the LGN are segregated by eye input, the input to each K layer generally reflects the input to the primary layer just dorsal to it.

Another component involves the remaining 10% or so, mostly large ganglion cells that sample the photoreceptor mosaic more sparsely than the major

types involved in acquiring sensory information (Rodieck and Watanabe, 1993). Relatively little is known about the circuitry and receptive fields of these ganglion cells in primates. Most involve complex dendritic trees that integrate both ON and OFF information about light contrast and their central projections are similar to those of other mammalian species. There are no less than nine subcortical nuclei distributed within 6 major regions that provide recipient zones for axon collaterals leaving the retina (reviewed in Leventhal et al., 1981 and Rodieck & Watanabe, 1993). Some of these ganglion cells may send collaterals to multiple nuclei, many of which provide projections back to the muscles of the eye for a variety of functions, including the coordination of eye movements and the setting of the circadian rhythm that contributes to the modulation of retinal physiology. In this review we will focus on the retino-geniculate-cortical pathway. For comprehensive information concerning areas outside of this pathway, the reader is referred to more specialized reviews (Rodieck, 1979; Kaas and Huerta, 1988; Rodieck, 1998).

LATERAL GENICULATE NUCLEUS

Anatomy

The LGN is about the size and shape of large peanut, situated in the posterior-most quarter of the thalamus. The LGN on each side of the thalamus receives input about the contralateral visual hemifield from the retina of both eyes, ipsilaterally from the temporal retina and contralaterally from the nasal retina (for general overview see Wurtz & Kandel, 2000). This input is anatomically segregated into six primary layers, each about 500 μm thick, with layers 1, 4, and 6 (numbered ventral to dorsal) receiving contralateral input and layers 2, 3 and 5 receiving ipsilateral input. The number of LGN neurons that receive retinal input and project to striate cortex is 1.0-1.5 million (Blasco et al., 1999; Hendry and Reid, 2000), about the same number of retinal ganglion cells that project to the LGN. (Spear et al., 1996) Thus, a 1:1 relationship between retinal ganglion cell and LGN relay neuron is usually presumed, though this is difficult to assess due to large variability in the numbers of ganglion cells and LGN cells between animals (Spear et al., 1996). Layers 1-2 comprise the ventral one-third of the LGN and contain about 10% of the cortical-projecting neurons to striate cortex. Because the bodies of these neurons are large, layers 1-2 are called magnocellular (or simply M). In contrast, layers 3-6 comprise the dorsal two-thirds of the LGN and contain about 80% of the LGN relay neurons. The bodies of these neurons are small by comparison, and layers 3-6 are termed parvocellular (or

P). The remaining 10% of the LGN relay neurons distribute non-uniformly, mostly within the intercalated layers sandwiched just ventral to each of the six primary M and P layers but also within small clusters within the primary layers. These cells can be visualized by neurochemical means (Hendry and Yoshioka, 1994) and are termed koniocellular (or K) because of their small size (Casagrande and Kaas, 1994; Hendry and Reid, 2000).

The relative number of M, P and K cells in the LGN reflects the nature of their retinal inputs. The population of P cells is the most numerous because most of these receive input from a midget ganglion cell, while the population of M cells is more sparse because many (but probably not all) receive input from a parasol ganglion cell (Perry et al., 1984). The small number of K cells, probably 3-5% (Calkins and Sterling, 1999), receives input from the small bistratified ganglion cell (Martin et al., 1997). Other types of ganglion cell project to each of the M, P and K populations, each with a unique morphology and pre-synaptic circuitry (Rodieck and Watanabe, 1993).

Functional Properties

The receptive fields of LGN neurons have center-surround organization reflecting the characteristics of the ganglion receptive fields providing their input (Hubel, 1960; Kaplan et al., 1990). Thus, neurons in the magnocellular layers of the LGN differ from those in the parvocellular layers by faster conduction velocities, greater luminance contrast sensitivity and greater contrast gain control (Derrington & Lennie, 1984). Furthermore, the parvocellular neurons show high spatial resolution, prefer lower temporal frequencies (Derrington and Lennie, 1984; Levitt et al., 2001), and have concentric color-opponent receptive fields, while the magnocellular neurons respond better to higher temporal and lower spatial frequencies, and their responses are spectrally broadband, and not affected by chromatic stimulus modulations (Wiesel and Hubel, 1966; Schiller and Malpeli, 1978; Schiller and Colby, 1983; Derrington et al., 1984). Thus, the main distinguishing characteristics between these neurons are chromatic opponency and differences in the spatiotemporal range of response properties (Figure 6.5). It should be pointed out that there is a large degree of overlap in spatiotemporal properties of the two subdivisions of the LGN and under many conditions the two classes of neurons give very similar responses to the same stimuli (Spear et al., 1994; Levitt et al., 2001). The functionally distinct magnocellular and parvocellular fibers from the LGN project to

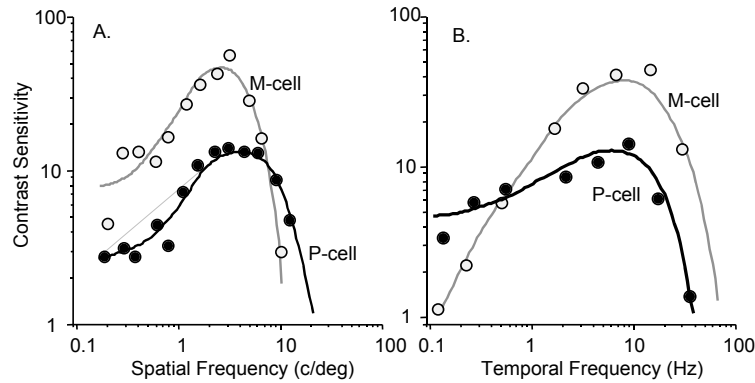


Figure 6.5. Spatiotemporal sensitivity of P and M neurons recorded from the LGN of the macaque monkey. Spatial (A) and temporal (B) contrast sensitivity of representative parvocellular (P-cell) and magnocellular (M-cell) neurons. Contrast sensitivity was taken as the reciprocal of the contrast that produced a criterion modulation of discharge on 50% of trials (usually about 10 spikes/sec). Each spatial and temporal sensitivity function was measured with sinusoidal gratings set at an optimal temporal or spatial frequency, respectively. The M cells have higher peak sensitivity to contrast and respond to higher temporal frequencies than the P cells. On the other hand, the P cells respond to higher spatial frequencies and show higher sensitivity at the lowest temporal frequencies. Note substantial overlap in the range of spatial and temporal frequencies to which the two classes of neurons respond. Replotted from Derrington and Lennie (1984).

different sublamina of layer 4 in striate cortex and this anatomical segregation of processing of different For years, similarities between the properties of retinal and LGN receptive fields have been used to categorize LGN as a passive relay station for signals on their way to cortex. However, recent physiological studies suggest that LGN is not a simple, passive relay of information to cortex but instead is involved in many dynamic processes that could affect the nature of the information relayed to cortex (Sherman and Guillery, 1996). These studies showed that LGN and other thalamic relay neurons exhibit two response modes: tonic and burst (Sherman, 1996). Based on the properties of the two response modes Sherman proposed that the burst mode is better suited for stimulus detection while the tonic mode for faithful transmission of visual stimuli (Sherman, 2001). He also proposed that the mechanism for switching between the two modes is under the control of afferents from the visual cortex and/or the brain stem and that the LGN contains the necessary intrinsic circuitry to accomplish this switch. This circuitry consists of a large number of inhibitory interneurons (Wilson, 1993), excitatory inputs from layer 6 of striate cortex (Casagrande & Kaas, 1994), as well as inputs from the parabrachial region of the brain stem and the thalamic reticular nucleus (Erisir et al., 1997). This organization allows LGN to play a more active role in transmitting and gating the information reaching visual cortex.

Effects Of Selective Lesions

Effects of lesions restricted to the P or M layers in the LGN reflect the spatiotemporal properties of the lesioned regions. For example, lesions restricted to the

magnocellular zone produce dramatic deficits in luminance contrast sensitivity for higher temporal and lower spatial frequencies (Schiller et al., 1990; Merigan et al., 1991a) measured with flickering or moving gratings (Figure 6.6 B), but no loss in sensitivity for chromatic stimuli (Merigan and Maunsell, 1990) (Merigan et al., 1991a) or for luminance contrast sensitivity when measured with stationary stimuli (see Figure 6.6A). These results correlate with the physiological studies of individual parasol cells in the retina and M cells in the LGN that show high contrast sensitivity for high temporal and low spatial frequencies. Although the effects of M lesions did not appear to have a specific effect on motion perception (Merigan et al., 1991a), the spatiotemporal characteristics of the deficit support a role for the magnocellular pathway in feeding signals to cortical streams for motion processing (Merigan and Maunsell, 1993).

In contrast, selective lesions of the parvocellular zone produce a fourfold decrease in visual acuity, cutting off sensitivity to higher spatial frequencies (Merigan et al., 1991b). Furthermore, the parvocellular lesion also results in a dramatic loss of both red/green and blue/yellow chromatic sensitivity (Merigan, 1989; Schiller et al., 1990) confirming the unique role of parvocellular neurons in carrying chromatic signals to cortex. However, one must keep in mind that the lesions included the population of K cells embedded within the dorsal two-thirds of the LGN, some of which are likely to receive inputs from the small bistratified ganglion cell implicated in processing of blue/yellow signals (Calkins and Sterling, 1999). The loss of these neurons could have contributed to the profound loss of chromatic contrast sensitivity reported by Merigan (1989).

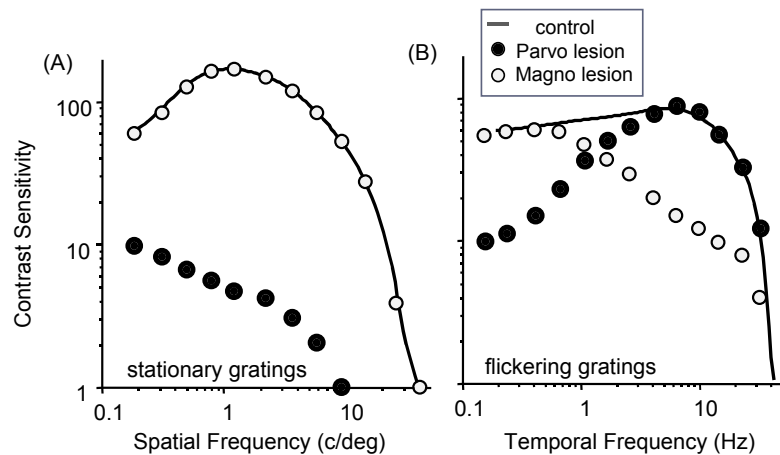


Figure 6.6. Visual loss after selective lesions of the magnocellular and parvocellular layers in the LGN. Monkeys discriminated between vertical and horizontal sinusoidal gratings presented in a portion of the visual field affected by the lesion. Contrast sensitivity (reciprocal of contrast threshold) was measured over a range of spatial and temporal frequencies. When the measurements were performed with stationary gratings (A), the parvocellular lesion resulted in a substantial loss in sensitivity to a wide range of spatial frequencies, which increased with spatial frequencies and a large loss in visual acuity. Under these conditions, the monkeys with the magnocellular lesions showed no sensitivity loss. When contrast sensitivity was measured with gratings flickering at various temporal frequencies (B), the magnocellular, but not the parvocellular lesions, resulted in a loss in sensitivity but only at intermediate and higher temporal frequencies. Adapted from Merigan and Maunsell (1993).

CORTICAL PROCESSING

The information provided by the three major types of ganglion cells arrives in visual cortex largely segregated. The functionally distinct magnocellular and parvocellular fibers from the LGN project to different sublamina of Layer 4 in striate cortex and this anatomical segregation of processing of different aspects of visual information continues to a greater or lesser extent throughout visual cortex. Neocortex contains at least 32 distinct areas identified as areas involved in processing of visual information (Felleman and Van Essen, 1991). A subset of these areas and a simplified diagram of major visual cortical pathways are shown in Figure 6.7.

The information about visual motion and spatial location generated at the earliest stages of cortical processing is directed for further elaboration into the *dorsal visual stream*, while shape, color, and texture information flow into the *ventral visual stream*. The two visual pathways originate in segregated subregions of primary visual cortex (V1) and continue to be largely distinct at the next stage of processing, in area V2, until they separate into the pathway streaming dorsally toward parietal cortex and the pathway streaming ventrally towards the temporal lobe. The former has been termed the “motion” or “where” pathway, while the latter “color and form” or “what” pathway (Ungerleider & Mishkin, 1982). Below we outline the functional organization and properties of the

most important and best understood components of the two pathways.

Primary Visual Cortex (Striate Cortex; V1)

Anatomy

The first stage of cortical processing of visual signals takes place in area V1, also called striate cortex because of the prominent stripe of white matter (“Stria Gennari” or the line of Gennari) running through layer 4. It is a large region that in the macaque monkey occupies an area of 1200 mm² in the occipital lobe or about 12% of entire neocortex (Felleman & Van Essen, 1991). The three types of inputs from the LGN to V1 (parvocellular, magnocellular and koniocellular) terminate in separate subdivisions within layer 4 (see Figure 6.4). The magnocellular and parvocellular fibers project to separate sublamina within layer 4C, layers 4C α and 4C β respectively (Hendrickson et al., 1978; Blasdel & Lund, 1983), thus maintaining their anatomical segregation. The koniocellular neurons from the intercalated laminae in the LGN terminate in layers 2/3 in regions with characteristic pattern of labeling for enzyme cytochrome oxidase, termed blobs (Horton, 1984; Livingstone and Hubel, 1984), as well as in layer 1 (Hendry & Reid, 2000).

Most of V1 output is directed to the adjacent area V2 (Livingstone & Hubel, 1983; Rockland & Pandya, 1979), although it also sends direct projections to MT (the middle temporal area; Boyd & Casagrande, 1999; Maunsell & van Essen, 1983), an area specialized for

processing visual motion (see below). V1 sends projections back to the LGN, to the pulvinar, a visual thalamic region implicated in control of attention, and to the superior colliculus (Casagrande & Kaas, 1994; Ungerleider, Galkin, & Mishkin, 1983). In addition, V1 maintains connections with a wide range of other cortical and sub-cortical regions (Kennedy & Bullier, 1985).

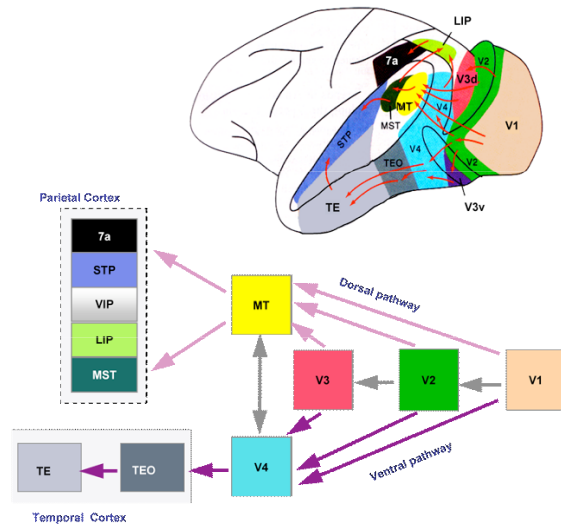


Figure 6.7. Visual areas in monkey cortex. The diagram of the monkey brain shows the location of cortical areas and their primary connections. The *dorsal* and the *ventral visual pathways* streaming towards the parietal and temporal lobes are shown in a simplified diagram. All the connections between cortical areas are largely reciprocal. The diagram of the monkey brain has been adapted from Farah et al. (1999).

Functional Properties

V1 contains a retinotopic representation of the entire contralateral visual field with a disproportionately large number of neurons devoted to processing of information provided by the foveal region of the retina (Dow et al., 1981; Azzopardi & Cowey, 1993). Thus, 6-9 cones located near the fovea are represented by 1 mm of cortex, while the same number of cones located 20 deg from the fovea are represented by a region of cortex that is about 5 times smaller (Dow et al., 1981; Van Essen et al., 1984). This expansion of the foveal representation, referred to as cortical magnification, is characteristic of many cortical visual areas and indicates allocation of additional neural circuitry for processing of information in the central portion of the visual field. This magnification may in part be a reflection of the great number of ganglion cells serving foveal cones (Wassle et al., 1989).

Receptive fields in V1 representing the fovea are quite small and increase with eccentricity in a manner that is roughly inversely proportional to cortical

magnification (Dow et al., 1981; Hawken and Parker, 1991). Thus, foveal receptive fields can be as small as 1-2 min of arc, about the diameter of a single cone, and as large as 60 min of arc at 20° eccentricity (Figure 6.8).

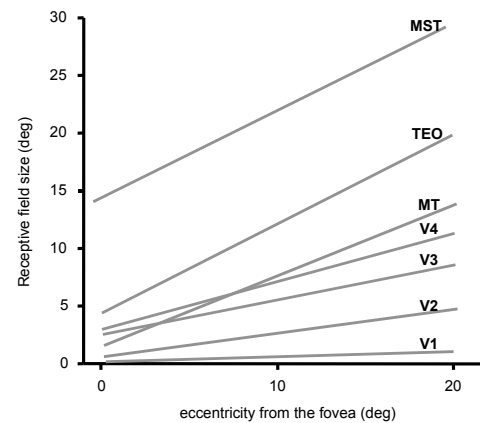


Figure 6.8. Receptive field sizes in visual cortical areas along the dorsal and ventral streams. Receptive fields are smallest in the foveal region in area V1 and increase with distance from the fovea. At subsequent stages of cortical analysis, receptive fields become larger and also increase with eccentricity from fovea. The data are taken from Dow et al. (1981), Desimone & Ungerleider (1986), and Felleman & Van Essen (1987).

Although the size of a cortical receptive field has always been considered one of its most stable features, recent studies revealed that it can be modulated by some properties of its optimal stimulus (e.g. contrast) as well as by the visual and behavioral context in which this stimulus is presented (e.g. Bakin, Nakayama, & Gilbert, 2000; Ito & Gilbert, 1999; Sceniak et al., 1999)(Figure 6.9). Such effects demonstrate the dynamic nature of cortical neurons, a phenomenon most likely mediated by the feedback projections arriving in V1 from subsequent levels of cortical analysis (Ito & Gilbert, 1999).

A number of features not seen in the preceding stages of analysis, emerge in striate cortex. These features include selectivity for stimulus orientation, size, depth, and the direction of stimulus motion and represent the first stage of processing leading to the perception of form and motion.

Sensitivity to Contrast; Spatiotemporal Filtering

One of the fundamental properties of retinal ganglion cells is center/surround organization, a feature that allows the detection of variations in luminance or chromatic contrast across space. Neurons in the magnocellular pathway are exquisitely sensitive and

show reliable responses to contrasts as low as 1%, while of parvocellular neurons require higher contrasts

(Derrington and Lennie, 1984) (see Figure 6.5).

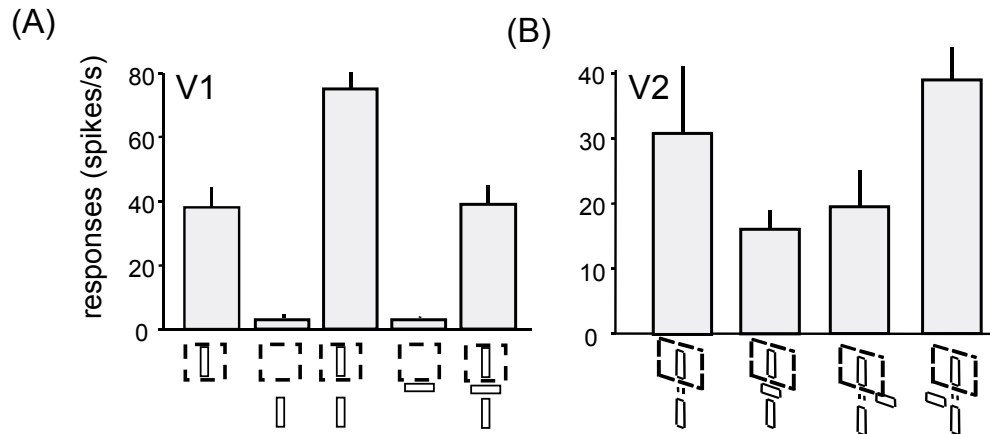


Figure 6.9. Stimuli outside of the classical receptive field affect responses of orientation selective cortical neurons. A. Responses of a V1 neuron to a bar of preferred orientation placed inside the receptive field (dashed square) are facilitated when a stimulus of the same orientation is placed outside of the receptive field. When the horizontal bar interrupts the contour formed by the two separated bars of the same orientation, the effect of facilitation induced by the bar outside the receptive field is blocked. B. Responses of a V2 neuron to a bar of preferred orientation in the receptive field are also facilitated by the stimulus of the same orientation placed outside the receptive field. However, this facilitation is blocked only when the horizontal bar is placed in the same depth plane or in the far depth plane (0.16° uncrossed disparity) relative to the two vertical bars. However, when the orthogonal bar is placed in the near depth plane (0.16° uncrossed disparity), facilitation by the peripheral vertical vertical bar is reinstated. This effect illustrates that depth cues provided by stimuli from outside of the receptive field can have strong modulatory effects on responses of cortical neurons at early stages of cortical processing and implicates neurons in area V2 in three-dimensional representation of surfaces. Adapted from Bakin et al (2000).

These properties are reflected in the cortical layers receiving inputs from the two pathways, with neurons in 4C α receiving inputs from the magnocellular neurons showing higher sensitivity to contrast than neurons in 4C β . This segregation of regions of low and high sensitivity to contrast is also present in neurons located in more superficial layers, projecting outside of striate cortex. Thus, while most neurons in layers 2/3 have relatively low contrast sensitivity, there is a small population of cells clustering near the centers of the blobs (see below) with high contrast sensitivity, reminiscent of magnocellular LGN neurons (Edwards et al., 1995). These cells are likely to receive inputs from the K cells which have been shown to have contrast sensitivity close to that of M cells (Xu et al., 2000). This larger dynamic range in the population of neurons within the blobs suggests that these regions are well equipped for signaling stimulus contrast.

Measurements of contrast response are usually performed with drifting or flickering sinusoidal gratings presented at spatial and temporal frequencies that are optimal for a given neuron. Careful selection of spatial and temporal stimulus parameters is necessary because visual neurons in cortex respond to a limited range of spatial and temporal frequencies, i.e. they behave like spatiotemporal filters. With respect to the spatial parameters, V1 neurons show sharp attenuation at both low and high frequencies (see Figure 6.10) (De Valois et al., 1982), unlike LGN neurons, which show

high frequency cut-off but more modest attenuation at low frequencies (Derrington & Lennie, 1984).

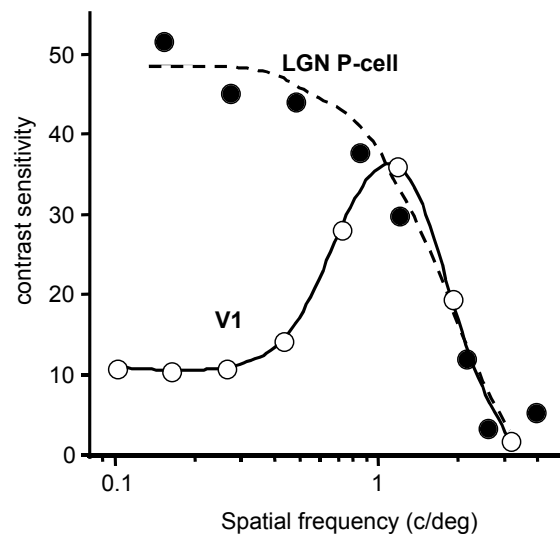


Figure 6.10. Spatial frequency selectivity of a neuron in LGN and V1. Responses of a LGN parvocellular neuron and a V1 simple color-luminance cell to equiluminant red/green gratings of different spatial frequencies. Note, that while P-cell shows no low spatial frequency attenuation, V1 cell is tuned to a narrow range of spatial frequencies. This spatial selectivity of color selective neurons

illustrates the integration of color and spatial information in V1. From Johnson et al (2001).

There is a correlation between the eccentricity, the optimal spatial frequency, high frequency cut-off and the size of the receptive field of a given neuron. For example, an increase in eccentricity that results in a two-fold increase in receptive field size is accompanied by a two-fold decrease in the optimal spatial frequency (Foster et al., 1985). However, not all regions in V1 have similar spatial tuning at a given eccentricity. For instance, neurons in the blobs appear to be tuned to low spatial frequencies and the optimal spatial frequency increases with distance from the blob (Born and Tootell, 1991; Edwards et al., 1995). Preferences for lower spatial frequencies have also been found in the sub-regions containing the majority of directionally selective neurons, upper layers 4 and layer 6 (Hawken et al., 1988). These neurons also show high sensitivity to contrast, a property characteristic of directionally selective neurons in MT (Sclar et al., 1990), the region that receives direct inputs from V1 (Hawken et al., 1988).

With respect to temporal characteristics, cortical neurons are similar to neurons encountered in the retina and the LGN and show broad tuning to temporal frequencies. However, while LGN neurons show preferences for relatively high frequencies of temporal modulation, 10-20 Hz, (Hicks et al., 1983), cortical cells respond better to lower temporal modulations, 3-8 Hz, showing little attenuation at low temporal frequencies (Foster et al., 1985).

Binocular Interactions

Information from the two eyes, segregated into separate layers in the LGN, remains segregated upon their arrival in layer 4C of striate cortex (Hubel and Wiesel, 1977). At this stage of cortical processing, the signals from the two eyes are processed separately and the neurons are grouped according to their eye of origin. These groupings, termed oculodominance columns (Figure 6.11A), are most prominent in layer 4C, but can be visualized as alternating bands across the entire thickness of cortex, becoming less apparent in layers above and below because of the intermixing of inputs from the two eyes. The amount of cortex devoted to processing the information from each eye is nearly equal for the central 20 deg of the visual field and the width of the alternating columns representing each eye is about 0.5 mm. The representation of the ipsilateral eye declines at greater eccentricity and eventually disappears with only the contralateral eye being represented (LeVay et al., 1985). The intermixing of the inputs from the two eyes in layers above and below layer 4 is reflected in the properties of neurons in these

regions, many of which respond best when both eyes are stimulated. Furthermore, many of these neurons are sensitive to the absolute retinal disparity or the difference in the position of a single stimulus in the two eyes (Poggio et al., 1988; Cumming & Parker, 1999; Livingstone & Tsao, 1999), an early stage of processing that leads to stereoscopic depth perception (Cumming & Parker, 2000).

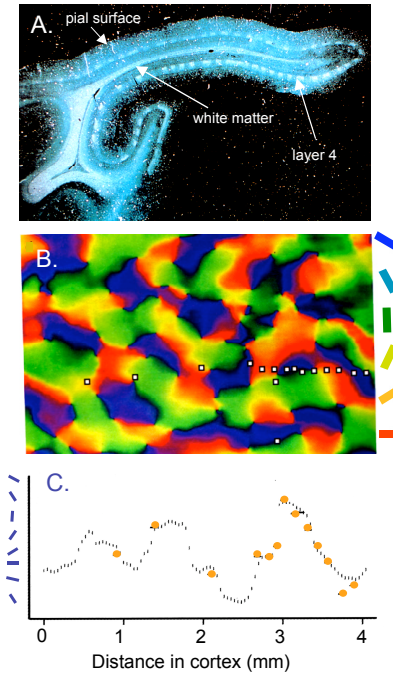


Figure 6.11. Organization of eye and orientation preferences in area V1.

A. Ocular dominance columns in monkey cortex seen as alternating bright and dark patches in layer 4 in a section cut perpendicularly to the surface. One eye of a monkey was injected with a radioactively labeled amino acid, which was taken up by cell bodies in the retina and transported to the LGN whose axons terminate in layer 4 in striate cortex. Areas in cortex that receive input from the injected eye are labeled and appear bright while the alternating unlabeled patches receive input from the uninjected eye. The white matter has a bright appearance because it contains labeled axons of LGN neurons.

B. Orientation columns in monkeys V1 revealed by optically imaging and comparing local changes in reflectance, which indicate activation. Imaging of the cortical surface was performed in anesthetized monkeys presented with stimuli of various orientations. Areas that were most active during the presentation of a particular orientation are indicated by the color bars. Complementary colors represent orthogonal orientations: red and green indicate maximal activity for vertical and horizontal orientations, while blue and yellow for right and left obliques.

C. Preferred orientation of neurons recorded with the microelectrode along the track indicated by the white squares in the optical image shown in B. The preferred orientations of the recorded neurons corresponds to those revealed with optical imaging. A. Adapted from Hubel & Wiesel (1979). B. and C. Adapted from Blasdel & Salama (1986).

Orientation Selectivity

Neurons in the input layers of striate cortex retain a concentric center/surround organization similar to that observed in the retina and LGN, whereas in other layers receptive fields become elongated and the neurons display selectivity for the orientation of the stimulus. Among orientation selective neurons, a subset of cells, termed *simple cells*, have receptive fields consisting of distinct excitatory and inhibitory sub-regions, while receptive fields of *complex cells* contain excitatory and inhibitory sub-regions that are intermixed (Hubel and Wiesel, 1968). Some orientation selective neurons, termed *hypercomplex cells* (or special complex cells) are also sensitive to the length of the optimally oriented stimuli and show inhibition if the bar extends outside of its receptive field (Hubel & Wiesel, 1977).

This inhibition, produced by the stimulus extending outside the classical receptive field, is not the only indication of active processes in the area surrounding the classical receptive field. A number of recent studies have shown that responses to stimuli placed in the receptive field are strongly modulated by the context in which this stimulus is presented. Most of these studies used oriented patterns centered on the classical receptive field surrounded by a large texture and found inhibitory or excitatory effects of the surrounding texture dependent on whether the elements in the surround matched the properties of the elements in the center (Knierim and van Essen, 1992; Nothdurft et al., 1999). In some cases, these influences were produced only by texture boundaries located close to the borders of the receptive field suggesting a role for V1 neurons in the detection of texture boundaries but arguing against the contribution of these neurons to the process of figure/ground segregation (Rossi et al., 2001). Since this contextual modulation often emerges a relatively long time after the stimulus onset it is likely to be the product of the influences of subsequent stages of cortical processing sending feedback projections to V1 (Nothdurft et al., 1999). These observations suggest that the mechanisms underlying texture segmentation and possibly figure-ground segregation may already be in place at a very early stage of cortical processing.

As for neurons with similar eye preferences, neurons with similar orientation preferences cluster into narrow columns extending perpendicularly from the cortical surface to the white matter (Hubel & Wiesel, 1977). Each column is about 30-100 μm wide and 2 mm deep. Neurons in these columns not only respond to the same orientation but also to stimulation of the same portion of the visual field. Along the cortical surface all axes of orientations are represented and the points where

neurons with different orientations meet form a characteristic “pinwheel” pattern (Obermayer and Blasdel, 1993) (Figures 6.11B and C). On average a region of 1 mm^2 on the surface of cortex contains all orientation preferences for a given point of visual space. This periodic pattern of orientation columns is interrupted by the cytochrome oxydase blobs regions prominent in layers 2/3, which contain cells that are not orientation selective, show some selectivity for color and respond to low spatial frequencies (Livingstone and Hubel, 1984; Edwards et al., 1995).

Together, columns representing each eye, orientation columns and the blobs for a given portion of the visual field form a unit, termed a *hypercolumn* (Hubel & Wiesel, 1977), each occupying 1 mm^2 of striate cortex. There is evidence that many columns and blobs with similar preferences are linked by long horizontal connections although there are also connections that would allow for the interactions between the compartments with different preferences (Yoshioka et al., 1996). These horizontal connections between individual compartments are believed to play a role in the integration of information over many millimeters of cortex (Gilbert et al., 2000).

Direction Selectivity

A feature emerging in V1 that has major implications for the ability to see object movement is selectivity for the direction of stimulus motion (Hubel & Wiesel, 1968). Directionally selective neurons fire vigorously to one direction of motion of an optimally oriented bar or grating and fire less or not at all when the same bar moves in the opposite direction. In the monkey, directionally selective neurons are present predominantly in layers 4C α and layer 4B, which sends projections to area MT (Hawken et al., 1988). Similarly to the magnocellular neurons in the LGN (Derrington & Lennie, 1984), these neurons are sensitive to low contrasts and have relatively poor spatial resolution (Hawken et al., 1988; Movshon & Newsome, 1996).

Response to Color

Chromatic signals from the three cone types, combined in an opponent fashion in the retina, arrive in layer 4C β in striate cortex from the parvocellular layers in the LGN. Thus, it is not surprising that chromatic properties of cortical neurons resemble those found in parvocellular neurons in the LGN (Derrington et al., 1984). Like the P cells, nearly all neurons in striate cortex show some degree of chromatic and spatial opponency, which is most commonly found in layers 4A, 4C β and in the blobs (Livingstone and Hubel, 1984; Ts'o and Gilbert, 1988; Lennie et al., 1990). A

less numerous group of color responsive neurons are those sensitive exclusively to stimuli defined by color differences (Johnson et al., 2001). These cells are largely non-oriented, respond to low spatial frequencies and are commonly found in blobs (Lennie et al., 1990; Leventhal et al., 1995; Johnson et al., 2001). A larger proportion of neurons respond robustly to stimuli defined both by color differences and by luminance (Johnson et al., 2001). This group of neurons, most commonly found in layers 2/3, is highly selective for stimulus form and is equipped to carry spatial information about color and luminance to other cortical areas (Johnson et al., 2001) (see Figure 6.10). Thus, these V1 neurons not only retain color information provided by the LGN but also add spatial selectivity that enables the detection of color boundaries.

There is recent evidence that V1 neurons not only retain but also amplify chromatically opponent signals arriving from the LGN producing a gradual change in color tuning (Cottaris & De Valois, 1998). This dynamic process, likely to involve intracortical circuitry, is reminiscent of a change in orientation tuning taking place about 30-45 msec after stimulus presentation, observed in neurons located in the output layers of striate cortex (Ringach et al., 1997).

Effects of V1 Lesions

In the primate most of the visual information is carried to cortex via the retino-geniculo-striate pathway, so it is not surprising that damage to V1 results in a profound visual loss (Weiskrantz and Cowey, 1967; Miller et al., 1980; Merigan et al., 1993). Although the loss appears to be nearly complete and humans with damage to striate cortex report inability to see anything in the affected portion of the visual field (Glickstein, 1988), rudimentary visual capacities appear to persist. Monkeys with V1 lesions can detect rapid flicker (Humphrey & Weiskrantz, 1967), discriminate simple colors (Schilder et al., 1972; Keating, 1979), track moving lights (Humphrey and Weiskrantz, 1967) and discriminate simple forms (Dineen and Keating, 1981). This residual visual function most likely depends on alternative projections that reach cortex via the superior colliculus and thalamus. For example, the minimal color vision that survives may depend on color-opponent P ganglion cells projecting to cortex through the pulvinar (Cowey et al., 1994). On the other hand, the coarse localization of light after V1 lesions may be maintained by the cortical areas receiving projections from the superior colliculus (Walker et al., 1995).

Area V2

Anatomy

Area V2 is a narrow strip of cortex located anterior and adjacent to area V1, on the surface of and inside the lunate sulcus (Zeki and Sandeman, 1976; Essen and Zeki, 1978). It contains topographically organized representations of the contralateral visual field (Gattass et al., 1981) and receives its major inputs from striate cortex (Kennedy and Bullier, 1985; Van Essen et al., 1986; Rockland, 1992). Although it also receives some projections from the LGN (Bullier and Kennedy, 1983) and pulvinar (Curcio and Harting, 1978), its activity appears to be driven mainly by the inputs provided by V1 neurons (Schiller and Malpeli, 1977; Girard and Bullier, 1989). As in area V1, the representation of the central 10 deg of the visual field is substantially expanded (Gattass et al., 1981). Area V2 projects topographically back to area V1, to areas V3, MT and V4, as well as to regions within parietal cortex, including areas MST, PO and VIP (Gattass et al., 1997).

Functional Properties

While many V2 receptive field properties resemble those found in V1, a number of new features emerge. Common to the two areas is the presence of selectivity for stimulus orientation and direction (Burkhalter and Van Essen, 1986). However, neurons in V2 have larger receptive fields (Gattass et al., 1981) (see Figure 6.8), prefer lower spatial frequencies and their spatial frequency tuning is somewhat broader than that of V1 neurons (Foster et al., 1985; Levitt et al., 1994a). While selectivity for stimulus orientation is present in more than half of V2 neurons (Zeki, 1978b), only a small proportion (15%) are selective for the direction of stimulus motion (Burkhalter and Van Essen, 1986; Levitt et al., 1994a). These directionally selective neurons are localized largely to the thick stripes (see below) and show somewhat higher contrast sensitivity (Levitt et al., 1994a), suggesting influences of the M-pathway.

Many neurons in V2 are sensitive to chromatic modulations (Burkhalter & Van Essen, 1986) and some show strong color opponent responses (Zeki, 1978b; Levitt et al., 1994a). There are similarities in chromatic sensitivity of V2 neurons with that observed in area V1, although some differences in tuning have been reported (Levitt et al., 1994a). There are also a greater proportion of color-oriented cells in comparison with V1, as well as neurons that exhibit color and disparity selectivity (Roe and Ts'o, 1997).

In contrast to area V1, most V2 cells are binocularly driven and many of these neurons are tuned to retinal disparity (Zeki, 1979; Hubel & Livingstone, 1987; Poggio, 1995). While most of these neurons are sensitive only to the absolute disparity, some respond to the *relative disparity* between different locations in

the visual field, a property absent from V1 neurons (Cumming and Parker, 1999). The emergence of neurons sensitive to relative disparity, a property upon which stereopsis depends, suggests that some V2 neurons may be providing signals to support depth perception (Cumming and DeAngelis, 2001).

Another feature to emerge in area V2 neurons is a robust response to illusory contours, first observed by Peterhans and von der Heydt (1989), although there is some evidence of neuronal responses to illusory contours in area V1 (Grosfeld et al., 1993). Such responses are indicative of neurons “filling-in” the information about missing contours, a process requiring some level of contour integration. V2 neurons have also been shown to respond to illusory contours induced by depth cues and these responses are present even with cues located beyond the classical receptive field, suggesting a role of long-range horizontal connections within area V2 (Bakin et al., 2000) (see example in Figure 6.9).

In addition to these properties, a selectivity of V2 for complex shapes has also been reported suggesting that an amount of integration of stimulus features encoded in area V1 is likely to take place in V2 neurons (Kobatake and Tanaka, 1994; Hegde and Van Essen, 2000). All these features suggest that the information provided by V2 neurons may play a role in coding of surface properties including contours, opacity, transparency, and relative depths.

Functional and Anatomical Segregation

The spatial segregation and clustering of receptive field properties characteristic of area V1, is also present in V2. The first insights into the anatomical and functional organization of this region were provided by the metabolic marker cytochrome oxidase which revealed a characteristic pattern of labeling consisting of a series of stripes (Livingstone & Hubel, 1984; DeYoe & Van Essen, 1985; Hubel & Livingstone, 1987; Olavarria & Van Essen, 1997). These stripes, consisting of dark thin and thick regions separated by lightly stained pale stripes, have also been visualized by optical imaging (Malach et al., 1994; Roe and Ts'o, 1995). The visual map of V2 consists of three distinct maps, with every location represented once in each of the thin, pale, and thick stripes; associated with neurons selective for color, orientation and disparity respectively (Zeki & Shipp, 1987; Roe & Ts'o, 1995). This anatomical segregation of the three modalities is not entirely complete as demonstrated by the presence of neurons selective for more than one modality. In fact, studies utilizing optical imaging combined with single neuron recordings revealed sub-compartments within individual stripes, specific for color, form and disparity (Ts'o et al., 2001). These findings argue

against the notion that processing of color, orientation and disparity is strictly localized to specific types of stripes. This is supported by the fact that the thick stripes in V2, known to receive inputs from layer 4B in V1, the magnocellular output layer, also receives inputs from layer 4A, the parvocellular output layer. Another interesting feature of projections supplied by pyramidal V1 neurons is their relatively extensive spread across V2 and the possibility that they interconnect individual stripe-like compartments in V2, providing an anatomical substrate for interactions between segregated channels in V1 (Levitt et al., 1994b). Furthermore, the intrinsic organization within V2 is such that all three cytochrome oxidase rich compartments are interconnected by horizontal connections (Levitt et al., 1994b; Malach et al., 1994). This anatomical intermixing of signals from the two pathways suggests that V2 may play a role in combining these signals, a notion supported by many receptive field properties encountered in this region.

Effects of V2 Lesions

While a number of studies have examined the effects of lesions on prestriate cortex, a region which in addition to V2 includes a number of other cortical areas, only one study examined the effects of lesions limited to area V2 (Merigan et al., 1993). This study reported depressed contrast sensitivity for orientation discrimination (measured with gratings defined by luminance or color) but not for the discrimination of the direction of motion, tested with rapidly moving stimuli. In addition, V2 lesions also profoundly and permanently disrupted the discrimination of complex form. This profile of visual loss is consistent with receptive field properties characteristic to that area and suggests that neurons in area V2 play an important role in processing of complex form and color but have a lesser role in motion perception.

Area V3

Anatomy

Area V3, a narrow strip of cortex located immediately anterior to V2, contains a representation of the central 40 deg of the contralateral visual field split into the ventral (V3v) and the dorsal (V3d) portions representing the upper and lower quadrants respectively (see Figure 6.7) (Essen & Zeki, 1978; Zeki, 1978d). Although the ventral and dorsal subdivisions of V3 encompass a single representation of the visual field, they differ in their pattern of connectivity (Van Essen et al., 1986) as well as in their receptive field properties, with V3d having a higher incidence of directionally selective neurons but lower number of color selective cells (Burkhalter and Van

Essen, 1986). Because of these differences, Burkhalter et al (1986) argued that these areas should be treated as separate visual areas and termed the dorsal region, V3 and the ventral region, VP (ventral posterior area). Recently, Kaas & Lyon (2001) disputed the idea of splitting these regions into separate visual areas and proposed an alternative scheme that included a single but redefined area V3. Although the issue of what specifically constitutes area V3 is important, the details of this controversy are outside the scope of this chapter and we will focus here on the results of recordings performed in this general region treating V3d and V3v together

This region receives major inputs from layer 4B of V1 and projects to areas MT, MST and VIP (Felleman et al., 1997b; Beck & Kaas, 1999), suggesting an association with the dorsal visual stream. However, V3 also receives inputs from V2 and is strongly interconnected with V4, the major component of the ventral visual stream (Beck & Kaas, 1999). Because of this pattern of connectivity, V3 is in a good position to serve as a site where the integration of various visual signals can occur.

Functional Properties

The properties of V3 neurons support the notion that this region may be one of the sites of integration between the visual signals carried by the two major functional streams. Unfortunately, only a small number of physiological studies examining visual receptive field properties have been performed on this region and those that did recorded from anesthetized animals (e.g. Gegenfurtner, Kiper, & Levitt, 1997). While the receptive fields of V3 neurons are larger than those found in V2 (Felleman and Van Essen, 1987; Gattass et al., 1988), they share a number of similar properties with V2 neurons, including a high incidence of orientation selectivity (80%) and similar orientation tuning (Gegenfurtner et al., 1997). On the other hand, V3 neurons prefer lower spatial and higher temporal frequencies and exhibit a higher sensitivity to contrast than V2 neurons (Gegenfurtner et al., 1997). These properties, together with the relatively high incidence of directional selectivity (nearly 60%) and the presence of selectivity for binocular disparity (Felleman and Van Essen, 1987) suggest a role in processing of motion information. Indeed, Gegenfurtner et al (1997) found that some directionally selective neurons in V3 respond to the motion of a plaid pattern rather to its components, a feature characteristic of many MT neurons and indicative of higher level motion processing (Movshon et al., 1985).

In addition to motion and depth analysis, nearly half of all neurons in V3 show selectivity for color (Burkhalter and Van Essen, 1986; Gegenfurtner et al.,

1997). It is noteworthy, that many of the neurons responding to color also show directional selectivity and a substantial number of V3 neurons responds show directional selectivity to isoluminant gratings. This interaction between color and motion, in addition to motion integration, suggests that area V3 represents an important stage in processing of visual information. These properties and the connections with areas MT and V4, the key mid-level components of the dorsal and the ventral cortical pathways, places V3 at an important stage in the analysis of the visual scene.

Area V3A

Van Essen & Zeki (1978) described a distinct region, located between areas V3 and V4 containing separate visual field representation, which they labeled area V3A. This region receives projections from area V2, projects to area V4, contains a representation of both the upper and lower visual quadrants, and has also been referred to as the posterior intraparietal area (PIP) (Colby et al., 1988; Felleman et al., 1997b).

Very few functional differences have been found between areas V3 and V3A. These differences include the finding that neurons in V3 become unresponsive to visual stimuli when V1 is removed, whereas a third of neurons in V3A remain responsive (Girard et al., 1991). The activity of neurons in V3A has been shown to be modulated by the direction of gaze (Galletti and Battaglini, 1989), and some of the direction selective neurons respond better to real motion across the retina rather than motion induced by a stationary stimulus when the eye moved (Galletti et al., 1990).

Parallel Functional Streams

The inputs from the P and M pathways are segregated into different cortical layers in striate cortex, and an anatomical segregation of neurons with similar properties is also apparent in area V2. However, the segregation within the visual system becomes most pronounced at the subsequent stage of cortical processing, in areas V4 and MT. At this stage, the two areas give rise to two distinct cortical streams, the ventral and dorsal pathways. The *ventral pathway* has been termed the "color and form" or the "what" pathway (Maunsell & Newsome, 1987) because in earlier studies both color and shape selectivity appeared to be most prominent in the physiological responses of neurons in the two main components of this stream; area V4 and inferotemporal cortex. The *dorsal pathway*, consisting of area MT and areas within posterior parietal cortex, has been termed "the motion" or the "where" pathway because of the prevalence of directionally selective neurons and the evidence for encoding of spatial location within this pathway.

Below we provide a brief overview of the major properties of the regions within the ventral and dorsal streams and the current view of their role in visual function.

VENTRAL VISUAL STREAM

Area V4

Anatomy

Area V4, first identified by Zeki (1971), is located in a region anterior to the lunate sulcus. It receives direct projections from areas V1, V2 and V3 (Zeki, 1978c; Yuki and Iwai, 1985; Nakamura et al., 1993), sends strong projections to area TEO in inferotemporal cortex, and has reciprocal connections with a number of other areas across the visual system (Tanaka et al., 1990; Distler et al., 1993). Anatomical modularity, prevalent in area V2 in the form of thin, thick and pale stripe regions, is not as apparent, although the projections from the thin and pale stripe subdivisions of V2 are distinct and there is evidence of a modular organization within V4 that reflect these inputs (Felleman et al., 1997a; Xiao et al., 1999). There is also evidence of clustering of neurons with similar preferred orientation and size (Ghose and Ts'o, 1997).

Functional Properties

Area V4 contains a complete representation of the contralateral visual field with an expanded representation of its central portion (Gattass et al., 1988). The receptive fields are well defined but are larger than those encountered in areas V1, V2 and V3 (Desimone and Schein, 1987; Gattass et al., 1988). Many of the properties encountered in area V4 are reminiscent of those found in primary visual cortex. Thus, many V4 neurons are tuned for stimulus orientation and show selectivity for the length and the width of oriented bars (Desimone and Schein, 1987; Cheng et al., 1994). In addition, about a third of V4 neurons show selectivity for the direction of stimulus motion (Desimone and Schein, 1987; Ferrera et al., 1994) and the majority are selective to binocular disparity (Hinkle and Connor, 2001). While V4 neurons respond selectively to many of the same features as V1 neurons, a number of more complex properties suggesting specialization for the analysis of complex form emerge. For example, Gallant et al. (1996) reported that V4 neurons are selective not only for conventional Cartesian gratings, but many respond preferentially to more complex polar and hyperbolic stimuli. Pasupathy and Connor (1999) found strong selectivity for specific stimulus contours, such as angles and curves, and showed a bias towards convex

contours, a feature that could account for perceptual preferences for convex forms, and a recently reported sensitivity to texture and selectivity to shading suggests the involvement of V4 neurons in the extraction of shape from shading (Hanazawa & Komatsu, 2001). An example of selective responses of V4 neurons to complex textures is shown in Figure 6.12. Together with sensitivity to binocular disparity, these features could enable V4 neurons to use stereoscopic cues to extract object information.

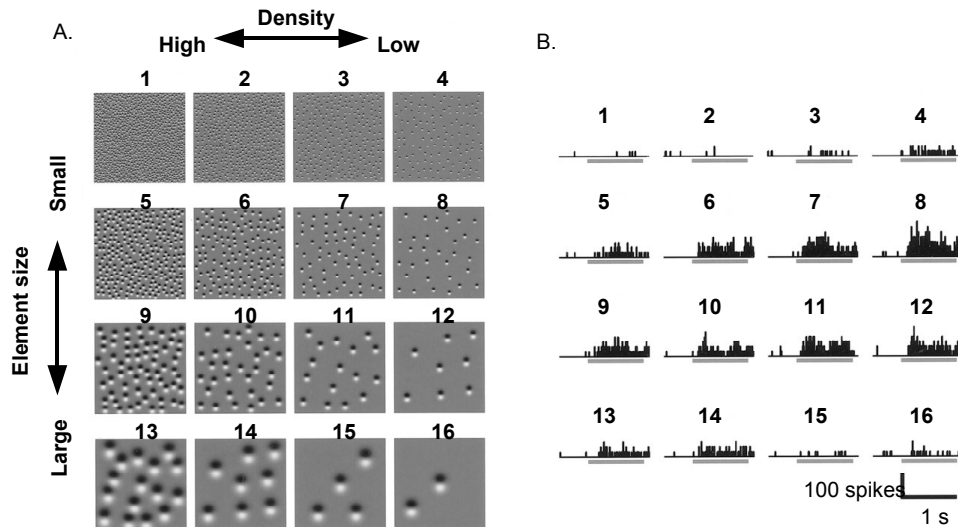
From the time area V4 was first described, it had been thought of as the color-processing area (Zeki, 1971). However, subsequent work has argued against this specialization. Although many V4 neurons show some wavelength sensitivity and a small proportion are color-biased or color-opponent, similar properties have been observed in neurons in other areas of visual cortex (Desimone et al., 1985). It remains to be seen whether V4 neurons show color constancy, one of the critical features of color vision.

Effects of V4 Lesions

A number of studies have examined the effects of lesions of this area on form and color discrimination and the results, for the most part, support its unique contribution to processing of form, as suggested by single unit recordings. These studies have shown that the loss of area V4 results in relatively modest and often transitory deficits in the discrimination of size and shape of simple forms (Heywood & Cowey, 1987; Walsh et al., 1992b; Schiller, 1993). Monkeys with V4 lesions can discriminate the orientation of simple gratings at normal levels as long as the gratings are at relatively high contrasts, are not masked by noise and are defined by luminance or color (De Weerd et al., 1996; Merigan, 1996). However, the same lesions produce severe and permanent deficits in tasks involving discrimination of illusory contours, 3-D forms, textures, as well as groupings (De Weerd et al., 1996; Merigan, 1996, 2000). These effects are quite selective, since when the contours are defined by motion, luminance or color, the effects of V4 lesions were minimal (De Weerd et al., 1996).

Lesions of V4 also affect some aspects of color vision although these effects are relatively modest. Walsh and colleagues reported largely transient deficits of color discrimination and modest deficits in color constancy (Walsh et al., 1992a; Walsh et al., 1993). They also reported that perception of color categories was unaffected by the absence of V4 neurons and suggested that these categories are established by chromatic mechanisms at earlier stages of cortical processing. Other studies have also reported relatively minor disruptions of hue discrimination thresholds and modest deficits in chromatic contrast sensitivity (Dean,

1979; Heywood et al., 1992; Merigan, 1996). These



results support the notion that while V4 represents

Figure 6.12. Responses of V4 neurons to texture patterns. A. Texture stimuli. In each row, the density of the elements doubled with each step. In each column, the size of the elements doubled and the density decreased by one-fourth with each step from top to bottom. Across all stimuli the spacing of the elements remained constant. B. Responses of a V4 cell tuned to density and size of the elements. Histograms show the responses to stimuli corresponding to those shown in A. Bars below histograms indicate the period of stimulus presentation. This neuron shows selectivity for textures with medium size elements of relatively low density suggesting it integration. From Hanazawa & Komatsu (2001).

an important step in processing of complex shape and texture, it is less likely to play a key role in processing of information about color.

Inferotemporal Cortex

Anatomy

Inferotemporal (IT) cortex, is the final processing stage of the ventral visual stream and is believed to play a key role in processing shape information. It consists of a posterior portion, area TEO, which in turn projects to the adjacent, more anterior portion, area TE. Area TEO receives its major inputs from V4 as well as from areas V2 and V3 (Distler et al., 1993). From there, visual information is sent to area TEO, which also receives a direct projection from V4 and from a number of areas in the ventral and anterior portions of the temporal lobe, including the hippocampus (Yukie and Iwai, 1988). This region also is reciprocally interconnected with ventral portions of prefrontal cortex (Seltzer & Pandya, 1989; Bullier et al., 1996), with the superior temporal polysensory area (STPa) which also receives projections from the dorsal pathway (see below), with parahippocampal regions (Shiwa, 1987) and with subcortical areas, notably the pulvinar (Baleydier and Morel, 1992), portions of the amygdala (Amaral & Price, 1984; Cheng et al., 1997), and with the basal ganglia (Middleton & Strick, 1996).

Functional Properties: Area TEO

Area TEO contains an orderly representation of the entire contralateral visual field with receptive fields that are somewhat larger than those in area V4, increasing with eccentricity from about 5 deg near the fovea to 60 deg in far periphery (Boussaoud et al., 1991). Inputs from V4 cluster to produce an apparent modular segregation within TEO with respect to color and shape selectivity (Felleman et al., 1997a). Many characteristics of TEO receptive fields are reminiscent of those found in V4 and earlier stages of cortical processing; there are many cells that respond selectively to simple features such as length, width, orientation and wavelength (Kobatake & Tanaka, 1994). However, selectivity for more complex patterns is also quite common (Desimone et al., 1984; Kobatake & Tanaka, 1994). The nature of this selectivity appears to be different from that encountered in TE (see below) since neurons show less invariance in their response to changes in the size and orientation of objects (Hikosaka, 1999).

Functional Properties: Area TE

In contrast to TEO, this region contains neurons with very large receptive fields that almost always include the fovea and extend into both visual hemifields covering as much as 40 deg of the visual field (Desimone and Gross, 1979; Boussaoud et al., 1991).

Its dorsal (TEad) and ventral (TEav) portions have slightly different connections and show some subtle differences in response properties (Martin-Elkins & Horel, 1992; Tamura & Tanaka, 2001), although for the purposes of this review we will treat them as a single area. The incidence of neurons responding strongly to complex stimulus features increases dramatically in area TE (Tanaka, 1997), and while some TE neurons show extreme selectivity for complex structures, such as faces (Desimone et al., 1984) (Figure 6.13A), other neurons are much less discriminating and respond strongly to a variety of complex patterns. Tanaka and colleagues (Tanaka, 1997) have shown that TE neurons with preferences for similar stimulus features cluster into overlapping columns, perpendicular to the cortical surface, and extending across all cortical layers. There are about 1300 of such columns, each extending over about 400 μ m (Tanaka, 1993) (Figure 6.13B).

Among novel features emerging in TE, and not present at earlier stages of cortical analysis, is response invariance. For example, there are neurons in TE with responses to complex stimuli that are not affected by large changes in the location of the stimulus in the visual (and receptive) field, or in retinal image size (Desimone et al., 1984; Ito et al., 1995; Hikosaka, 1999). Neurons in TE also respond to three-dimensional objects and develop selectivity for specific views of those objects, particularly for those that the monkey learned to recognize the familiar views of those objects (Logothetis and Pauls, 1995).

There is accumulating evidence that TE neurons acquire preferences to specific stimulus features through learning (Sakai and Miyashita, 1994; Logothetis et al., 1995; Kobatake et al., 1998). For example, it has been shown that exposure to a set of patterns during discrimination training increases the probability that TE neurons will respond maximally to these stimuli (Kobatake et al., 1998). The finding by Logothetis et al. (1995) that the selectivity of TE neurons is most pronounced for objects the monkey is able to recognize suggests that new receptive field properties can be acquired during active learning. This apparent ability of TE neurons to acquire new properties with learning has also been demonstrated in tasks designed specifically to test long-term memory for complex patterns (Sakai and Miyashita, 1994).

Another striking feature of TE neurons was revealed in experiments by Sheinberg and Logothetis (1997), who used perceptually ambiguous stimuli induced by binocular rivalry. They showed that the activity of the majority of IT neurons is determined by the perceptually dominant stimulus, a phenomenon only rarely observed at earlier stages of cortical analysis (Leopold and Logothetis, 1996). This activity, together

with the complex response properties described above, reinforces the importance of IT neurons in the processing and perception of complex shape and form.

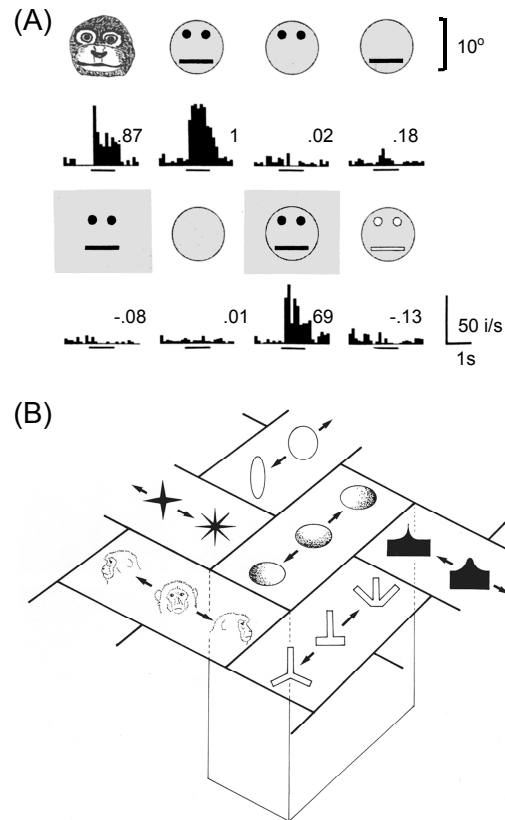


Figure 6.13. A. Response of a neuron in the anterior portion of inferotemporal cortex (TEO) to complex stimuli. The histograms show responses of the cell to each of the stimuli shown above. The line below each histogram indicates the time of stimulus presentation. The cell responded strongly to the face of a toy monkey and to a pattern consisting of two dots and a horizontal line arranged in a gray circle, a configuration resembling the face. Other stimuli, consisting of some but not all elements of these stimuli were ineffective in producing a response.

B. Schematic drawing of columnar organization in TE. This cortical region consists of columns in which cells respond to similar but not identical features. Cells in different columns respond to different features and each column extends across all cortical layers. The width of each column is greater than 400 μ m and it has been estimated that there are 1300 columns across the entire surface of TE. From Tanaka (1996).

Effects of IT Lesions

The role of IT in object recognition was first revealed in studies involving damage to this region over 50 years ago (Mishkin, 1954; Mishkin & Pribram, 1954) and numerous lesion studies performed since (for review see Merigan & Pasternak 2003). Many of these

studies reported deficits in the discrimination of complex forms as well as in the learning of new discriminations (e.g. Britten, Newsome, & Saunders, 1992; Huxlin et al., 2000). These deficits were often transient and only a few persisted after extensive retraining. A number of studies also examined the effects of IT lesions on color vision and found deficits in color discriminations that ranged from profound to relatively modest (e.g. Buckley, Gaffan, & Murray, 1997; Huxlin et al., 2000). As is the case with form discriminations, post-lesion training often resulted in improvements in color vision. On the whole, the effects of IT lesions are reminiscent of effects of area V4 lesions (see above) although in the case of color vision the deficits appear a bit more pronounced.

DORSAL VISUAL STREAM

Area MT

Although the dorsal visual stream originates in specific layers of striate cortex and occupies well-defined subregions (thick CO stripes) within area V2, it becomes truly distinct, both anatomically and functionally, at the level of the middle temporal area (MT) located in the superior temporal sulcus (STS). During the past 10-15 years, area MT has become one of the most studied mid-level processing areas in the visual system of primates. Because most of the physiological recordings from this area are carried out in monkeys performing behavioral tasks, this area has become a fertile ground for establishing links between neural activity, behavior and perception.

Anatomy

Area MT was first described and named by Allman & Kass (1971) in the Owl monkey. Subsequently, Zeki (1974) identified an equivalent area in the macaque monkey and, because of the selectivity of neurons in this area to image motion, named it the “motion area of the superior temporal sulcus” and later “V5” (Zeki, 1978a). In the macaque monkey, MT is located in the medial part of the posterior bank of the STS. It receives strong projections from layer 4B of striate cortex (Hawken et al., 1988), the recipient zone of the magnocellular pathway, and from the thick stripes of area V2 (DeYoe & Van Essen, 1985; Shipp & Zeki, 1989); both regions that contain a high incidence of directionally selective neurons. MT projects to the adjacent area MST (Desimone & Ungerleider, 1986), also rich in directionally selective cells, and provides inputs to other regions of parietal cortex (Gattass and Gross, 1981; Boussaoud et al., 1990). Together with these associated areas, MT constitutes an important component of the dorsal visual stream specialized for

processing of visual motion and spatial information. MT also maintains reciprocal connections with area V4 (Ungerleider & Desimone, 1986) allowing direct communication between the two streams, and interconnects with some areas in prefrontal cortex (Schall et al., 1995) as well as with a number of subcortical structures including the superior colliculus and pulvinar (Ungerleider et al., 1984).

Functional Properties

MT contains a complete representation of the contralateral visual field with a disproportionately large area devoted to central vision (Van Essen et al., 1981). Its neurons have relatively large receptive fields, similar in size to those of area V4 (Desimone & Ungerleider, 1986) (see Figure 6.8). Selectivity for the direction and speed of stimulus motion is the defining characteristic of the majority of MT neurons (e.g. Albright, 1984; Maunsell & Van Essen, 1983a) (Figure 6.14), and neurons with similar directional tuning are organized in columns (Albright, 1984). The majority of MT neurons respond best to the stimulation of both eyes, are selective for retinal disparity (Maunsell & Van Essen, 1983a; Tanaka et al., 1986; DeAngelis and Newsome, 1999) and neurons with similar disparities cluster into columns, which extend over the thickness of cortex (Figure 6.15). The two sets of columns, direction and disparity, seem to occupy the same subregions in MT, the relationship between them is still unclear (DeAngelis and Newsome, 1999).

Motion Integration

MT neurons display directional selectivity to smooth and sampled motion of random dots, bars (Figure 6.14) and gratings (Maunsell and Van Essen, 1983b; Mikami et al., 1986) as well as to more complex motion consisting of multiple motion vectors at the same part of the visual space (Albright, 1984; Britten et al., 1992b). This property of MT neurons was first demonstrated by Movshon et al. (1985) and later Rodman and Albright (1989), who compared responses to moving gratings of different orientations to plaid patterns consisting of two component gratings. They found that while some MT neurons responded only to the motion of the individual components of the plaid, other neurons appeared capable of coding the direction of the whole plaid pattern, independent of the motions of component gratings. In contrast, direction-selective neurons in striate cortex responded exclusively to the motion of the components to the plaid, rather to the direction of plaid motion. It is interesting that the behavior of these pattern-selective neurons in MT responding to the direction of the plaid matched the

percept reported by human observers viewing the plaid stimuli (Adelson and Movshon, 1982).

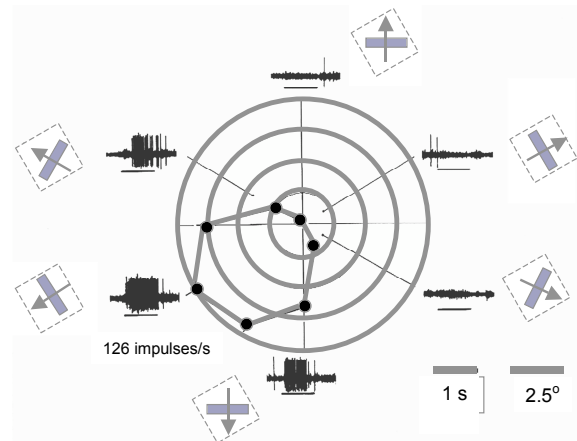


Figure 6.14. Direction selective neuron in MT. Small slits of light (gray bars) were moved in various directions across the receptive field (dashed squares) and responses to individual presentations of each direction of motion were recorded. The polar plot shows average firing rates in response to each direction. The horizontal line below each response trace represents the stimulus duration. This neuron shows strong preference for the motion to the left and down (firing rate, 126 impulses/sec) and did not respond to the opposite direction (to the right and up). Over 90% of neurons in MT show strong selectivity to stimulus direction, similar to that shown here. Adapted from Maunsell and Van Essen (1983a).

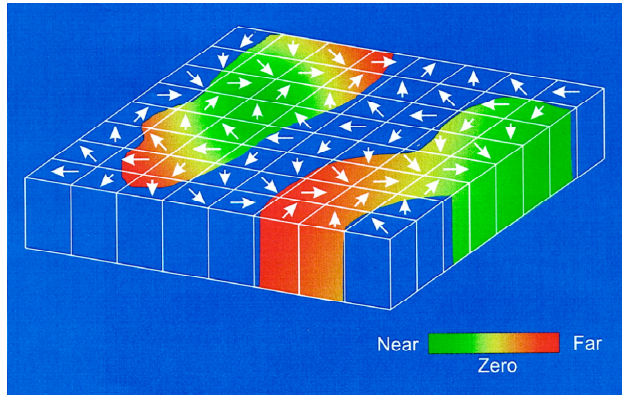


Figure 6.15. Columnar organization of direction and binocular disparity selectivity in MT. The surface of this slab corresponds to the surface of MT, and its height represents the thickness of cortex. Arrows denote the preferred direction of motion of MT neurons in each direction column. Preferred disparity is color coded, with green representing near disparities, red representing far disparities, and yellow indicating zero disparity. Blue regions denote portions of MT that have poor disparity tuning. From De Angelis and Newsome (1999).

These experiments demonstrate the emergence of neuronal properties that could be tied more directly to perception.

Subsequent studies have examined the responses of MT neurons to other types of complex motion, also consisting of multiple motion vectors presented in the same part of the visual space. For example, in contrast to V1 neurons, which respond equally well to non-transparent and transparent motion, responses of MT neurons to the motion of transparent surfaces formed by random dots moving in different directions are suppressed (Snowden et al., 1991). Similar suppression has been observed with a smaller number of elements moving in different directions within an MT receptive field (Recanzone et al., 1997). This suppression is reminiscent of the perception of motion transparency observed in human psychophysical experiments (Qian et al., 1994) and is an example of the way MT neurons deal with multiple directional vectors at the same spatial location.

Another example illustrating the integrative properties of MT neurons comes from studies utilizing stochastic random-dot stimuli consisting of coherently and randomly moving dots (e.g. Britten et al., 1992), in which the strength of motion is controlled by the proportion of spatio-temporally correlated dots. Britten et al. (1993) showed that the responses of MT neurons to such stimuli vary linearly with stimulus correlation suggesting linear pooling of local directional signals provided by earlier stages of motion analysis, most likely by striate cortex neurons. Another study involving random-dot stimuli containing multiple directions showed that responses of direction-selective neurons in MT reflect the sum of their responses to the individual motion components (Treue et al., 2000).

Finally, direction-selective MT receptive fields have strong antagonistic surrounds, which when stimulated by the same direction and/or speed as the excitatory center, show strong inhibition (Allman et al., 1985; Xiao et al., 1995). This property illustrates the ability of MT neurons to integrate local motion signals with the context in which this motion appears, suggesting a role in the detection of relative motion and in figure-ground segregation.

Processing of Depth

A large proportion of neurons in MT are tuned for depth (Maunsell and Van Essen, 1983a; Tanaka et al., 1986; DeAngelis and Newsome, 1999), and are found clustered according to preferred disparity (see Figure 6.15). These neurons appear to contribute to stereoscopic depth perception, as microstimulation of similarly tuned cells can bias the monkey's perceptual judgment of depth towards the preferred disparity (DeAngelis et al., 1998). Apart from depth perception, the disparity tuning of these neurons appears to be relevant to other perceptual phenomena. For example, a difference in disparity of the display consisting of

sheets of random dots create the percept of transparent motion (Qian et al., 1994; Bradley et al., 1995), and changing the disparity in the surround of the classical receptive field modulates not only the response of MT neurons to motion, but also the percept of the direction of motion (Bradley et al., 1998; Duncan et al., 2000). It has also been suggested that MT may be involved in extracting shape-from-motion (Buracas and Albright, 1996; Dodd et al., 2001), and while there is evidence of the interaction between motion and disparity signals in the same neurons (Bradley et al., 1995), MT neurons do not appear to be tuned to motion-in-depth (Maunsell and Van Essen, 1983a).

Processing of Color

Although the activity of MT neurons is strongly influenced by the magnocellular pathway (Maunsell et al., 1990), not known to carry color-opponent signals, many MT neurons maintain significant responses to motion of isoluminant stimuli (Gegenfurtner et al., 1994; Seidemann et al., 1999; Thiele et al., 2001). Furthermore, the presence of chromatic information has been shown to increase neuronal direction discrimination (Croner & Albright, 1999). While, chromatic signals reaching MT are much weaker than the luminance signals, the activity in MT to isoluminant gratings appears to be sufficient to explain the performance of monkeys in a color-based motion discrimination task (Thiele et al., 2001).

Relating Activity of MT Neurons to Perception

Newsome and colleagues have used stochastic random dot stimuli (see above) as a tool to study the relationship between the activity single neurons and behavioral performance (Britten et al., 1992; Newsome, Britten, & Movshon, 1989). They have found that single MT neurons are able to detect the direction of motion in such stimuli at nearly the same level as the monkeys performing the task. They concluded that only a small number of MT neurons are needed to explain the perceptual judgments made by the monkeys. Subsequently, Britten and Newsome (1998) examined directional tuning of MT neurons near psychophysical threshold and modified this view concluding that direction discrimination near threshold is likely to depend on a population of MT neurons with a wide range of preferred directions.

Other powerful evidence that monkeys use signals from MT during the performance of this task comes from microstimulation experiments (Salzman et al., 1990; Seidemann et al., 1998; Bisley et al., 2001). In these studies, low current stimulation of physiologically identified directional columns in MT applied during the presentation of random-dots at various levels of coherence, biased the animals decisions towards the preferred direction of the stimulated directional column (Salzman et al., 1990; Salzman et al., 1992). Bisley et al (2001) recently applied higher current stimulation during the performance of a discrimination task in which the monkey compared two directions of motion separated in time (see Figure 6.16A). When stimulation was applied during the presentation of the first of the two stimuli, the monkeys consistently reported that the stimulus was moving in the direction preferred by the stimulated neurons, irrespective of the true stimulus direction (Figures 16B and C). Furthermore, the monkeys reported motion in the preferred direction of the stimulated column even when the stimulus consisted of stationary dots. Thus, MT neurons appear to be the main source of information used by the monkeys to judge the directions of stimulus motion.

Effects of MT Lesions

Studies involving lesions of MT have largely confirmed the ideas about the role of MT in motion perception, as suggested by the neurophysiological and microstimulation experiments. Although some of the lesion effects were transient and showed substantial post-lesion recovery with training (Newsome and Pare, 1988; Rudolph & Pasternak, 1999), they were selective for the properties characteristic of MT neurons. Thus, direction and speed discrimination, motion integration as well as the ability to extract motion from noise were selectively affected by the damage to area MT (Newsome and Pare, 1988; Pasternak and Merigan, 1994; Rudolph and Pasternak, 1999; Bisley and Pasternak, 2000). Deficits in processing of speed information were also revealed by measuring saccades and smooth pursuit of the moving targets (Newsome et al., 1985; Dursteler et al., 1987; Schiller and Lee, 1994).

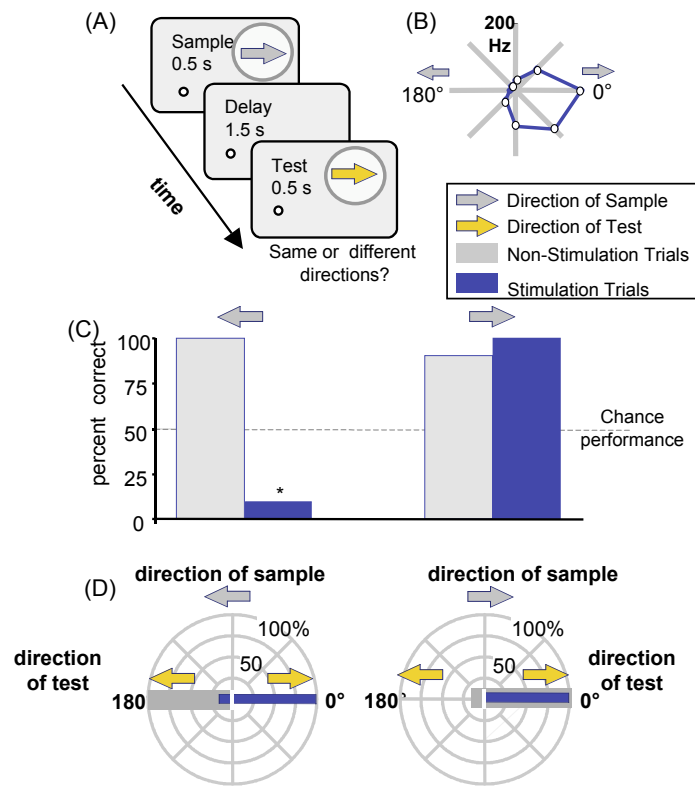


Figure 6.16. Microstimulation of a directionally selective column in MT.

A. Behavioral task. The monkeys compared two directions of moving random-dot stimuli presented in sequence and separated by a brief (1.5 sec) delay. They were rewarded for correctly reporting the two stimuli as moving in the same or different directions by pressing one of two push buttons. The two stimuli always moved either in the same or opposite directions and the directions of sample motion were selected on the basis of the preferred direction of the stimulated site in MT.

B. Direction selectivity profile of a representative site in MT measured by recording multi-unit activity. Note, that this site responds best to rightward moving stimuli.

C. Effect of microstimulation of the site in MT shown in B. Stimulation was applied during the entire duration of the sample on 25% of the trials. The performance during non-stimulation trials (gray columns) was nearly perfect for sample moving to the right (preferred direction) or to the left (null direction). During stimulation trials (blue columns) the monkeys performed at 100% correct when the sample moved rightward (columns on the right), but near 0% correct when sample moved leftward.

D. Analysis of trials in which the monkey equated the direction of the sample with the direction of the test ("same" trials). The axes on the polar plot indicate the direction of motion of the test stimulus (also indicated by the yellow arrows). The distance from the origin shows the percent of trials in which sample direction was equated with test direction. During non-stimulation trials, the monkeys equated sample and test almost every time the sample and test both moved to the right or to the left. During stimulation trials, the monkey always equated the sample with the rightward moving test, irrespective of the true direction of the sample. This suggests that the monkey interpreted signals produced by stimulation of rightward directional column as directional motion signals. From Bisley et al, 2001.

Area MST

Anatomy

Area MST, the medial superior temporal area, was first identified as the MT-recipient zone by Maunsell & van Essen (1983). It communicates with the far peripheral field representations of areas V1 and V2 as well as

with the parieto-occipital visual area of the dorsal pathway (Maunsell & van Essen, 1983; Boussaoud et al., 1990). MST consists of two functionally and anatomically distinct regions: dorsal (MSTd) and ventrolateral MST (MSTv or MSTl) (Tanaka et al., 1989; Tanaka and Saito, 1989).

Functional Properties

Neurons in MSTd have very large receptive fields and prefer motion of full-field stimuli (Desimone and Ungerleider, 1986; Saito et al., 1986; Tanaka et al., 1986), while cells in MSTl generally have smaller receptive fields and respond preferentially to motion of small objects (Tanaka, 1998). Properties of MSTd neurons suggest a role in integrating visual motion signals generated during the observer's movement through the environment, with eye-movement and vestibular signals (Andersen, 1997). On the other hand, neurons in MSTl are more likely to be involved in the analysis of object motion in the environment (Tanaka, 1998) and in the maintenance of pursuit eye movements associated with this motion (Komatsu & Wurtz, 1988).

Processing of Optic Flow

MSTd neurons have been implicated in the processing of "optic flow", the motion of the visual world perceived by observers during their own movement through the environment. This type of visual motion can be a source of information about the direction of self-motion (Gibson, 1994).

Neurons in MSTd respond to various types of motion of large-field flow patterns, such as expansion, contraction, rotation, translation or a combination of these (Tanaka & Saito, 1989; Duffy & Wurtz, 1991; Lagae et al., 1994). In response to full-field optic flow stimuli, many of these neurons have a preferred location of the focus of expansion (FOE) which may serve as a cue of the direction of heading (Duffy and Wurtz, 1997; Page and Duffy, 1999; Upadhyay et al., 2000) (Figure 6.17). These neurons often do not discriminate between the optic flow created by the movement of a subject and simulated optic flow (Duffy, 1998) and their responses are largely unaffected by eye or head movements (Bradley et al., 1996; Page & Duffy, 1999; Shenoy et al., 1999). Although it is still not clear how the visual cues resulting from self-motion are utilized, it appears that the computation of the direction of heading is likely to be represented in the population of MST neurons rather than at level of single neurons (Paolini et al., 2000).

Thus, MSTd has the machinery needed to extract and signal the direction of heading from optic flow stimuli (Lappe et al., 1996; van den Berg & Beintema, 2000). The evidence that the use of such information may depend on MST has been provided by Britten et al. (1998) who took advantage of clustering of neurons preferring the same direction of heading (Britten, 1998) and applied electrical microstimulation to them. This manipulation produced biased decisions about direction of heading provided by from optic flow stimuli. It

should be pointed out, however, that there is no direct evidence that this mechanism is actually utilized during self-motion. While there is some indication that humans use optic flow to control walking (Warren et al., 2001), there are much more conclusive data suggesting that rather than using optic flow, humans usually aim towards an object and correct their aim as they walk (Rushton et al., 1998).

Retinal Disparity and Object Motion

Some properties of MSTl neurons are reminiscent of neurons in MT. For example, in addition to similarly sized receptive fields, there are many neurons tuned for retinal disparity and some show a change in direction selectivity when disparity is changed (Roy et al., 1992; Eifuku and Wurtz, 1999; Takemura et al., 2001). Similarly to MT, neurons in this region have antagonistic surrounds and respond very strongly to object motion when the motion in the surround is in the opposite direction (Eifuku & Wurtz, 1998). This sensitivity to relative motion of objects suggests that these neurons may play a role in segmenting moving objects from backgrounds.

Involvement in Eye Movements

MSTd neurons have also been shown to participate in mechanisms underlying both voluntary and involuntary eye movements. They are active during smooth pursuit eye movements (Komatsu & Wurtz, 1988) and the ability to match the speed of the target during pursuit is affected by lesioning (Dursteler and Wurtz, 1988) and electrical stimulation of these neurons (Komatsu & Wurtz, 1989). MSTd neurons are also active prior to the ocular following response (OFR), an involuntary short-latency tracking eye movement, evoked by a sudden movement of a stable environment (Miles et al., 1986; Kawano et al., 1994; Takemura et al., 2000). Since these responses are also affected by MST lesions (Dursteler & Wurtz, 1988) it is likely that this area serves a role in the circuitry sub-serving OFR.

In sum, the properties of this important component of the dorsal visual stream point to its role in processing of motion information in active observers. Neurons in MSTd are capable of integrating visual information extracted during movement of the observer with signals related to eye and head movements (Andersen et al., 1999). On the other hand, MSTl may contribute to the ability to detect and pursue motion of small objects in complex environments.

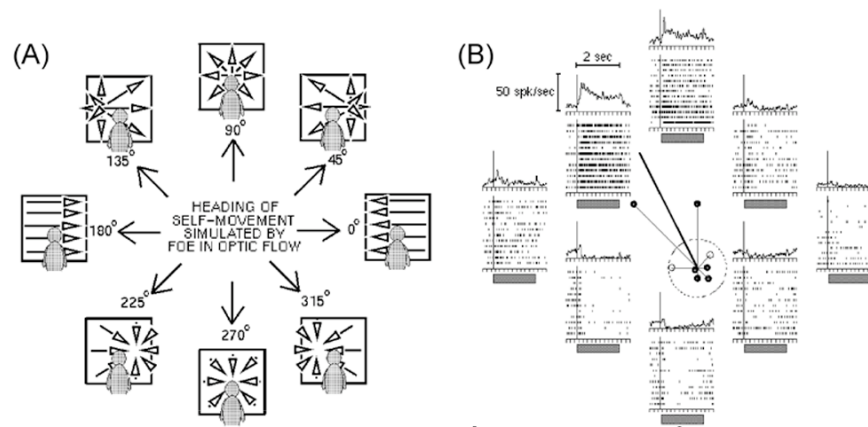


Figure 6. 17. Neuronal responses to Optic Flow in MST. Responses of a single neuron recorded in the medial superior temporal area (MST) of an awake rhesus monkey.

A. Eight optic flow stimuli were presented in a pseudorandom sequence. Each frame represents the $90^\circ \times 90^\circ$ rear-projection screen as viewed by a monkey (shaded figure) that is fixating a point at the center of the screen. The arrows in each frame illustrate the local direction of white dot movement on the otherwise black background of the screen. The focus-of-expansion (FOE) at the junction of the arrows is a cue about the simulated direction of self-movement. The large arrows indicate the heading direction of self-movement that is simulated by the adjacent optic flow pattern.

B. The responses of a neuron that showed a strong preference for the left-forward direction of simulated self-movement. Responses to repeated presentations of the optic flow stimuli are shown as spike rasters in which each vertical deflection indicates the occurrence of a neuronal action potential. Spike density histograms graph the average firing rate across the presentation period (shaded bar) for the stimulus at the corresponding position in A. The polar plot at the center includes eight limbs (narrow lines) having directions that indicate the simulated heading direction in a stimulus, and lengths that indicate the relative firing rate evoked by that stimulus. The control firing rate, recorded during trials in which no optic flow stimulus was presented, is indicated by the radius of the circle. The balls at the end of each polar limb indicate whether the response represented by that limb was significantly different from the control firing rate. The net vector (bold line) is the sum of the stimulus vectors and indicates the preferred direction of that response and the strength of that directional preference (Courtesy of C. J. Duffy, 2001).

Area LIP

Anatomy

LIP, the lateral intraparietal area, and its contribution to visually guided behavior, has received a lot of attention in recent years. Studies examining the properties of LIP neurons have focused on its role in encoding of representation of visual space, its role in planning eye movements and in spatial attention. It receives inputs from a number of cortical regions including V2, V3, V3A, V4, MT, MST, TEO and TE (Andersen et al., 1985; Andersen et al., 1990a; Blatt et al., 1990). It is reciprocally interconnected with areas VIP and 7a in parietal cortex (Seltzer & Pandya, 1986; Blatt et al., 1990), with prefrontal and premotor cortex, as well as with the superior colliculus and pulvinar (Cavada & Goldman-Rakic, 1989; Schall et al., 1995).

Functional Properties.

LIP contains a representation of the contralateral visual field and more than half of its neurons are devoted to processing stimuli in a region of about 6°

around the fovea (Ben Hamed et al., 2001). Receptive fields in LIP are larger than those in MT, although they are well defined and increase in size with eccentricity from about 5° near the fovea (Ben Hamed et al., 2001).

Neurons in LIP have a number of properties not seen at earlier levels of visual processing. While they respond to the onset of visual stimuli (Robinson et al., 1978), they also show memory activity in tasks requiring saccadic eye movements to remembered spatial locations (Gnadt & Andersen, 1988; Barash et al., 1991a, b). There is also evidence that the activity of LIP neurons is modulated by the position of the eye in the orbit (Andersen et al., 1990b) and that these neurons store information not only in eye-centered (Duhamel et al., 1992) but also in body-centered coordinates (Snyder et al., 1998).

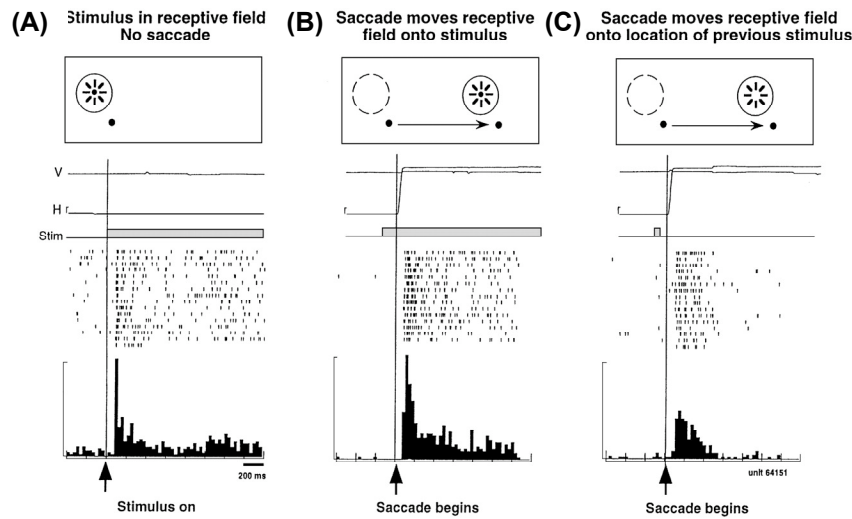


Figure 6.18. Remapping of memory trace activity in area LIP. The top of each panel shows the task, followed by the vertical and horizontal eye traces. The thick gray bar shows the duration of the visual stimulus. The activity in single trials is illustrated by the tick marks and the histogram shows the mean activity in 25ms bins. A. During fixation, this LIP neuron responds to the stimulus in the receptive field. B. The response following a saccade that moves the stimulus onto the receptive field. C. The response following a saccade that moves the location where the stimulus had flashed onto the receptive field. The stimulus was presented for 50 msec and is extinguished before the saccade begins. The response is thus to a memory trace that has been remapped from the coordinates of the initial eye position to those of the final eye position. Adapted from (Colby and Olson, 1999).

Another intriguing feature of LIP neurons is that the spatial representation of the remembered stimulus is dynamic and shifts to the corresponding retinal location around the time of a saccade (Duhamel et al., 1992) (Figure 6.18). Thus, neurons in parietal cortex update the retinal coordinates of remembered stimuli to anticipate the upcoming eye movement. This remapping, important for maintaining continuous representation of the visual world during eye movements, is not unique to LIP, since it has also been observed in other visual areas, including areas V2, V3 and V3A (Nakamura & Colby, 2000, 2002).

These properties, together with observations showing that LIP neurons fire in preparation for a saccade, lead to the hypothesis that the memory activity preceding the saccade represents an intention to make a saccade to the remembered location (Mazzoni et al., 1996; Andersen et al., 1997; Platt & Glimcher, 1997; Snyder et al., 1997). According to this hypothesis, LIP activity is indicative of the role of LIP in sensory-motor transformations that

take place in preparation for action. An alternative hypothesis is based on results showing that the visual and memory responses are modulated by the salience and behavioral significance of visual stimuli (Colby et al., 1996; Gottlieb et al., 1998; Powell and Goldberg, 2000). This hypothesis suggests that the level of activity in LIP is used by the brain to allocate attention to the region of greatest activity, whether it is driven by a salient stimulus, such as a saccade target, or by top-down mechanisms. Whether LIP is involved in motor planning, attention, or both, the activity of these neurons provides the opportunity to study neural correlates of cognitive behavior (Shadlen & Newsome, 1996; Leon & Shadlen, 1998; Platt & Glimcher, 1999; Shadlen & Newsome, 2001) (Figure 6.19).

Some neurons in LIP also display properties more common in other visual areas, such as selectivity for stimulus shape (Serenio and Maunsell, 1998) and the direction of stimulus motion (Eskandar and Assad, 1999). However, it is not clear whether these response properties represent a role in processing this information,

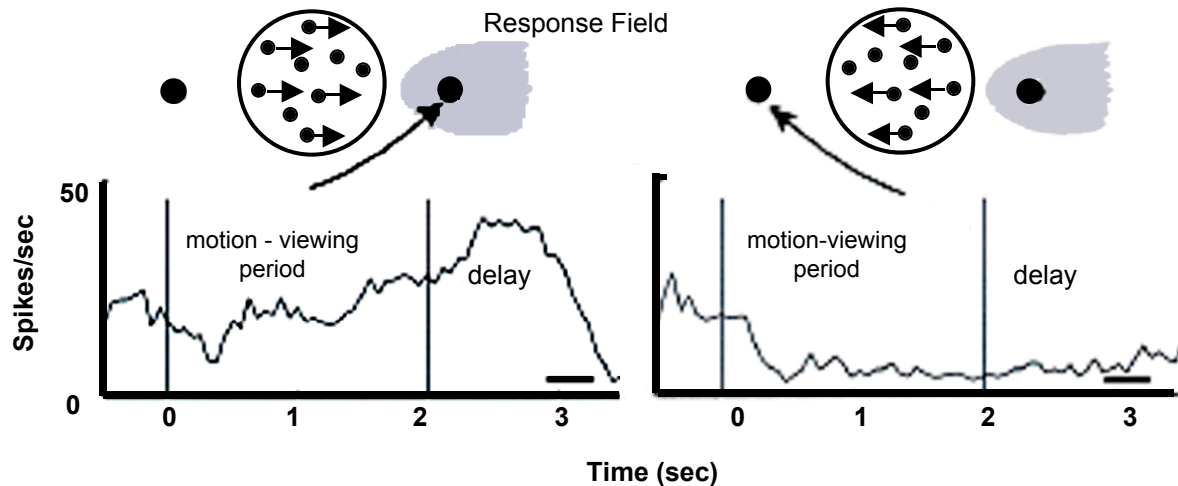


Figure 6.19. Responses of a LIP neuron during the performance of a direction discrimination task. The monkey judged the direction of motion of a dynamic random dot stimulus by making saccadic eye movements to one of two targets (black spots). The targets were placed either in the LIP receptive field or in a remote location. The plots show the activity of an LIP neuron during the presentation the visual motion stimulus and during the delay prior to the saccade. The authors suggest that this activity represents a neural correlate of the decision process that involves integration of sensory signals toward a decision appropriate for guiding movement. From (Leon and Shadlen, 1998).

or whether these are just the remnants of signals from the multitude of areas that project to LIP. In summary, LIP neurons appear to carry visual, memory and saccade related signals which are modulated by the behavioral significance of the stimulus, suggesting that they are involved in sensory-motor transformations taking place in preparation for goal oriented eye movements and possibly in the allocation of visual attention.

Area VIP

VIP, the ventral intraparietal area, has prominent connections from MT, MST and FST, but unlike LIP, it receives little if any inputs from the ventral pathway (Boussaoud et al., 1990; Colby et al., 1993). This, as well as its interactions with other parietal areas, suggests that VIP plays a role exclusively in the dorsal stream. Receptive fields of neurons in this area are similar in size to those found in LIP (Duhamel et al., 1998) and show selectivity for optic flow (Colby et al., 1993; Schaafsma and Duysens, 1996). The responses of many VIP neurons are modulated by eye position and individual neurons can encode information in eye-centered coordinates through to head centered coordinates (Duhamel et al., 1997; Bremmer et al., 1999). Some neurons have been found to prefer stimuli that are close to the animal (Colby et al., 1993) and most of these cells also respond to tactile stimuli in congruent locations on the head to the visual receptive fields (Duhamel et al., 1998). This has led to the suggestion that this

region is involved in a construction of a multi-sensory head centered representation of near personal space (Duhamel et al., 1998).

Area STPa

STPa, the superior temporal polysensory area, receives inputs from both visual streams (Boussaoud et al., 1990; Baizer et al., 1991) and has been proposed to be a region of convergence and integration of form and motion signals (Oram & Perrett, 1996). Its neurons respond to visual as well as somatosensory and auditory stimuli (Bruce et al., 1981), they have large, gaze centered, receptive fields and show selectivity to visual motion similar to that observed in areas MT and MST (Oram et al., 1993; Anderson and Siegel, 1999). Some neurons also respond particularly well to biological motion, such as that made by a walking person (Perrett et al., 1985; Oram and Perrett, 1996; Anderson and Siegel, 1998).

Area 7a

Area 7a constitutes the final stage in the hierarchy within the dorsal visual stream and is interconnected with a wide range of cortical and subcortical regions providing visual and visuomotor signals important for the execution of visually guided behavior. It receives inputs from areas LIP and MST as well as from other visually responsive areas in parietal cortex (Cavada and Goldman-Rakic, 1989; Andersen et al., 1990a). It sends ascending projections to prefrontal cortex (Selemon and Goldman-Rakic, 1988; Cavada and Goldman-Rakic, 1989; Neal et al., 1990) as well

as projections to inferotemporal cortex, to LIP and STPa, as well as to the basal ganglia (for review see Siegel and Read 1997). Neurons in area 7a have large receptive fields that are often bilateral (Blatt et al., 1990). They respond to visual stimuli (Mountcastle et al., 1975; Robinson et al., 1978) and are active during fixation and visual tracking eye movements (Sakata et al., 1983; Kawano et al., 1984; Bremmer et al., 1997). Since the activity of these neurons are largely not affected by changes in body or head position during saccades to specific retinal locations, it is likely that these cells encode information in world-referenced coordinates (Snyder et al., 1998).

Some neurons in area 7a possess properties similar to those encountered at preceding stages of processing in the dorsal visual stream. These neurons are sensitive to complex visual motion, exhibiting selectivity to rotational motion (Sakata et al., 1986; Sakata et al., 1994), to the optic flow patterns and its components (Read and Siegel, 1997; Siegel and Read, 1997; Phinney and Siegel, 2000).

A number of studies have shown that responses of 7a neurons are modulated by the behavioral relevance of the stimulus appearing in the receptive field (Robinson et al., 1978; Mountcastle et al., 1981). A salient or behaviorally relevant object appearing in a non-attended location can enhance the activity of a neuron, while the same object appearing in the attended region often reduces its activity (Steinmetz et al., 1994; Constantinidis and Steinmetz, 2001). This phenomenon, also observed in LIP neurons (Powell and Goldberg, 2000), suggests that area 7a together with LIP may play a role in the control of spatial attention.

Other Vision Related Areas in Parietal Cortex

There are a number of less studied visually responsive areas in parietal cortex and little is known about their role in visually guided behavior. Some of these areas appear to be associated with somatosensory and motor cortical areas. Among these areas are V6 and V6A (Galletti et al., 1996; Nakamura et al., 1999), the medial intraparietal area (area MIP), the medial dorsal parietal area (area MDP) and area 7m (Johnson et al., 1996; Ferraina et al., 1997; Luppino et al., 1999).

Area FST contains visually responsive neurons with large receptive fields at the center of gaze and, unlike STPa, has limited directional selectivity (Desimone and Ungerleider, 1986). Little is known about the function of this area, which appears to lie at a similar level to MST within the visual hierarchy.

COGNITIVE MODULATION OF CORTICAL ACTIVITY: VISUAL ATTENTION

With the use of a number of simple but effective behavioral paradigms, such as change blindness and attentional blindness (Rensink, 2000) it has become clear that visual attention is necessary for the construction of the visual world we perceive. These behavioral paradigms demonstrate that without the ability to allocate attention, detecting even large changes in the visual world becomes difficult. In the laboratory, directing attention to a specific location of the visual field speeds up detection and increases sensitivity to visual stimuli presented at that location (Bashinski & Bacharach, 1980; Posner, 1980; Yantis & Jonides, 1984; Bowman et al., 1993). Neurophysiological correlates of this enhancement have been found in many visual areas, including areas V1 (Roelfsema et al., 1998; Ito and Gilbert, 1999), V2 (Luck et al., 1997; Reynolds et al., 1999), V3A (Nakamura & Colby, 2000), V4 (Fischer & Boch, 1981; Moran & Desimone, 1985; McAdams & Maunsell, 1999; Reynolds et al., 2000), and areas MT and MST (Treue & Maunsell, 1996; Seidemann & Newsome, 1999).

Effects of attention on processing of visual stimuli have been found already at the level of primary visual cortex. For example, Ito and Gilbert (1999) have shown that while the attentional state of an animal has no detectable effect on responses to oriented stimuli placed in the receptive field, it affects neuronal activity when these stimuli are surrounded by flanking lines placed outside the receptive field. The authors proposed that this modulation is accomplished by feedback connections from higher order cortical areas.

The enhancement of neural activity associated with the demand of the behavioral task has been studied most extensively in area V4. Neurons in this area show enhanced responses to visual stimuli when they become the target of a saccade (Fischer and Boch, 1981; Moore et al., 1998) or when a single stimulus used by the monkey in the discrimination task is placed in the receptive field (Motter, 1994b; McAdams and Maunsell, 1999; Reynolds et al., 2000). This attentional enhancement is greatest when the discriminative stimulus is presented at near threshold contrasts resulting in an increase in neuronal sensitivity to contrast (Reynolds et al., 2000) (Figure 6.20).

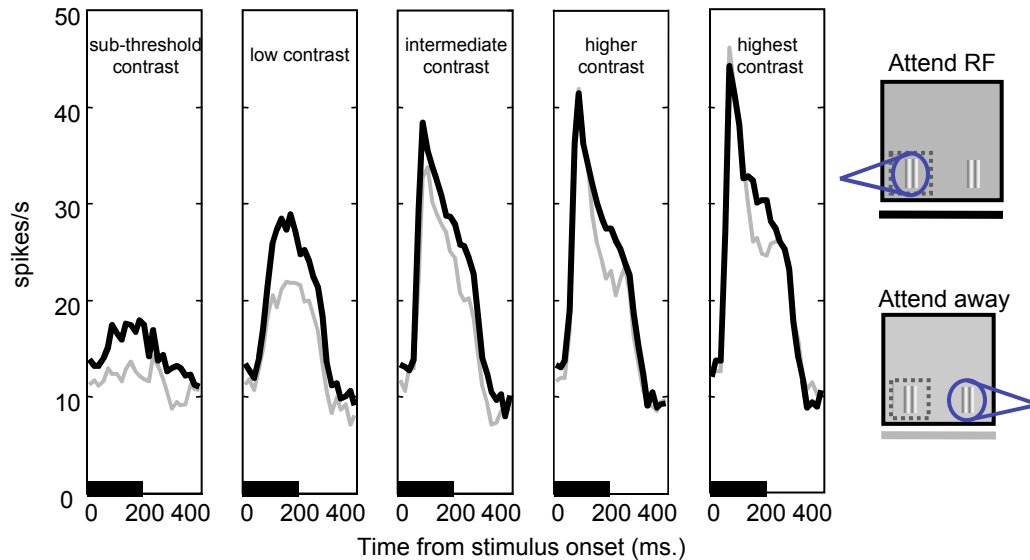


Figure 6.20. Effect of attention on sensitivity to contrast in area V4. Responses of V4 neurons to stimuli across a range of luminance contrasts were recorded while the monkey discriminated a target stimulus appearing in a sequence of non-targets. The bar-shaped patches of grating were simultaneously presented at two locations: one in the receptive field (indicated by a dashed square) and the other at an equally eccentric position in the opposite hemifield. The monkey performed a discrimination task either with stimuli in the receptive field (“attend RF”) or with stimuli away from the receptive field (“attend away”). Each panel shows the response at a particular contrast, averaged across the population of 84 neurons. Black lines show average response to the attended stimuli, gray lines response to the ignored stimuli. Attention caused a greater increase in the response at low contrast than at high contrast. Thus, attention increased sensitivity of V4 neurons to contrast. Adapted from Reynolds et al (2000).

Attentional effects on neuronal firing are even more pronounced when two stimuli are placed within the receptive field of a V4 neuron, in this case the response is primarily driven by the attended stimulus (Moran & Desimone, 1985; Reynolds et al., 1999). These observations lead to a hypothesis that within the circuitry of extrastriate cortex, there is a mechanism that gates out the unattended stimulus (Desimone, 1998), and that this gating may be due to the interaction between neighboring receptive fields (Connor et al., 1997). In animals with lesions of V4, attention appears to be automatically allocated to the most salient stimulus, suggesting that the mechanism that controls the gating may include neurons within V4 (Schiller, 1993; De Weerd et al., 1999).

Although earlier studies identified area V4 and the ventral visual stream as one of the main sites of attentional influences on visual processing, a number of recent studies have demonstrated similar influences in visual cortical areas within the dorsal visual stream. For example, Treue and Maunsell (1999) have shown that directing attention to the receptive field in areas MT and MST results in an increase in neuronal firing. This effect was more pronounced when two spots moving in the preferred and the non-preferred direction were placed in the receptive field and attention was directed from the non-preferred to the preferred direction. In a

subsequent study, Treue & Martinez-Trujillo (1999) have demonstrated that attention increases the gain of direction-selective neurons. These effects are similar to those found in area V4 and show that attention enhances the representation of the attended stimuli and reduces the influence of unattended stimuli.

COGNITIVE MODULATION OF CORTICAL ACTIVITY: VISUAL MEMORY

Traditionally, sensory cortical areas have not been thought of as regions playing a role in retaining information about the stimuli they process. However, there is now accumulating evidence of the active involvement of sensory areas in neuronal circuitry underlying temporary storage of this information (Fuster, 1997). This type of storage, often referred to as working memory, remains active for only a few seconds, and is distinct from long-term memory (Squire, 1987). Its major function is to briefly retain information to be used in specific tasks, a function fundamental to the successful execution of visually guided behaviors.

Much of the neurophysiological work studying the neural mechanisms of visual working memory has focused on IT, which represents a relatively advanced stage of processing within the ventral visual stream (Merigan & Maunsell,

1993). Such studies have reported that IT neurons of monkeys trained to remember visual properties of objects, maintain an elevated firing rate during the delay after a specific color, shape or location is presented (e.g. Fuster, 1990; Miller, Li, & Desimone, 1993; Miyashita & Chang, 1988). These results have been interpreted as evidence that these neurons may be involved in the short-term storage of information about stimulus form, color, or location. Neurons in V4, which provide a major input to IT, also show enhanced responses to previously cued visual stimuli (e. g. Ferrera et al., 1994; Motter, 1994b). Furthermore, there is also some evidence that lesions of V4 affect performance of some memory related tasks (Desimone et al., 1990; Walsh et al., 2000).

Within the dorsal visual stream, memory related activity has been reported in area 7a for motion (Ferrera et al., 1994) and in spatial memory tasks in areas 7a and LIP (Constantinidis & Steinmetz, 1996; Barash et al., 1991b), although it is not clear whether this latter activity represents short-term memory *per se*, or whether it is a neural mechanism used to track the spatial locations of previously identified objects of importance. Neurons in MT do not show the same sustained pattern of memory-related activity as neurons in 7a, V4 or IT (Ferrera et al., 1994). However, there is accumulating evidence that this area shows a pattern of activation during the delay indicative of its participation in storage of visual information (Droll et al., 2000). This observation is consistent with the suggestion provided by lesion and microstimulation studies that MT may be involved in storing the information it encodes (Bisley and Pasternak, 2000; Bisley et al., 2001).

CONCLUDING REMARKS

In recent years the visual system of non-human primates has become the system of choice in the study of neural mechanisms underlying visual perception. One reason is the apparent similarity in visual function between old-world monkeys and humans. The second reason is that the development of behavioral and neurophysiological procedures has provided an opportunity to record neural activity in monkeys that can be directly related to visually guided

behavior. These techniques have provided new insights into the properties of visually responsive neurons at various stages of cortical analysis. The first and perhaps most important realization that emerged from these studies is that visual cortical (and probably thalamic) neurons are not simply passive processors of any stimulus that appears on the retina, as long as the stimulus matches the preferences of its receptive field. There is now evidence that as early in processing as primary visual cortex, responses of neurons are defined not only by the properties of the visual stimulus but also by its behavioral significance. The modulation of neuronal responses by the behavioral significance of a stimulus has been well documented in areas V2 and V4, in MT, and in the posterior parietal cortex. The results reported by many of these studies suggest that some of the characteristics of cortical receptive fields established in experiments performed with anesthetized animals may have to be re-examined. Another feature of visual cortical neurons that emerged from combining neurophysiological recordings with behavioral testing is their ability to change their receptive fields as a result of training. This plasticity has, until recently, been considered to be the property of a developing brain, however it appears to be present in the adult inferotemporal cortex (Kobatake et al., 1998), and has recently been documented in striate cortex (Crist et al., 2001). There is also accumulating evidence that visual cortical neurons, particularly those at middle and later stages of analysis, are not only involved in processing visual information but also participate in circuits underlying its storage (see Fuster, 1995). These results further emphasize the dynamic and plastic nature of neural circuitry underlying processing of visual information. They also point to the continued participation of this circuitry in more cognitive processes (e.g. memory and learning), processes that until recently have been thought to be localized to regions outside of traditionally defined sensory systems.

These developments call for the application of approaches that would allow examination of the neural basis of visually guided behaviors by simultaneously monitoring the activity of wider brain regions. Functional magnetic resonance imaging (fMRI), is one such technique.

Introduced only about 10 years ago, it has become widely used in the study of neural activity-related signals associated with visual processing in humans (Courtney & Ungerleider, 1997; Wandell, 1999). The development of this approach with non-human primates, will provide an important tool for simultaneously examining neural activity in multiple brain regions during the performance of visual guided behaviors. Several laboratories recently began successful efforts in that direction (Dubowitz et al., 1998; Stefanacci et al., 1998; Logothetis et al., 1999). Another important approach to examining the activity of neuronal ensembles in multiple brain regions is simultaneous microelectrode recordings from multiple brain regions. This valuable tool has already been applied in several laboratories with some success (see Nowak et al., 1999; Varela et al., 2001) and holds great promise.

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