

Central Visual Pathways

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THE VISUAL SYSTEM HAS THE most complex neural circuitry of all the sensory systems. The auditory nerve contains about 30,000 fibers, but the optic nerve contains over one million! Most of what we know about the functional organization of the visual system is derived from experiments similar to those used to investigate the somatic sensory system. The similarities of these systems allow us to identify general principles governing the transformation of sensory information in the brain as well as the organization and functioning of the cerebral cortex.

In this chapter we describe the flow of visual information in two stages: first from the retina to the midbrain and thalamus, then from the thalamus to the primary visual cortex. We shall begin by considering how the world is projected on the retina and describe the projection of the retina to three subcortical brain areas: the pretectal region, the superior colliculus of the midbrain, and the lateral geniculate nucleus of the thalamus. We shall then examine the pathways from the lateral geniculate nucleus to the cortex, focusing on the different information conveyed by the magno- and parvocellular divisions of the visual pathways. Finally, we consider the structure and function of the initial cortical relay in the primary visual cortex in order to elucidate the first steps in the cortical processing of visual information necessary for perception. [Chapter 28](#) then follows this visual processing from the primary visual cortex into two pathways to the parietal and temporal cortex.

In examining the flow of visual information we shall see how the architecture of the cortex—specifically its modular organization—is adapted to the analysis of information for vision.

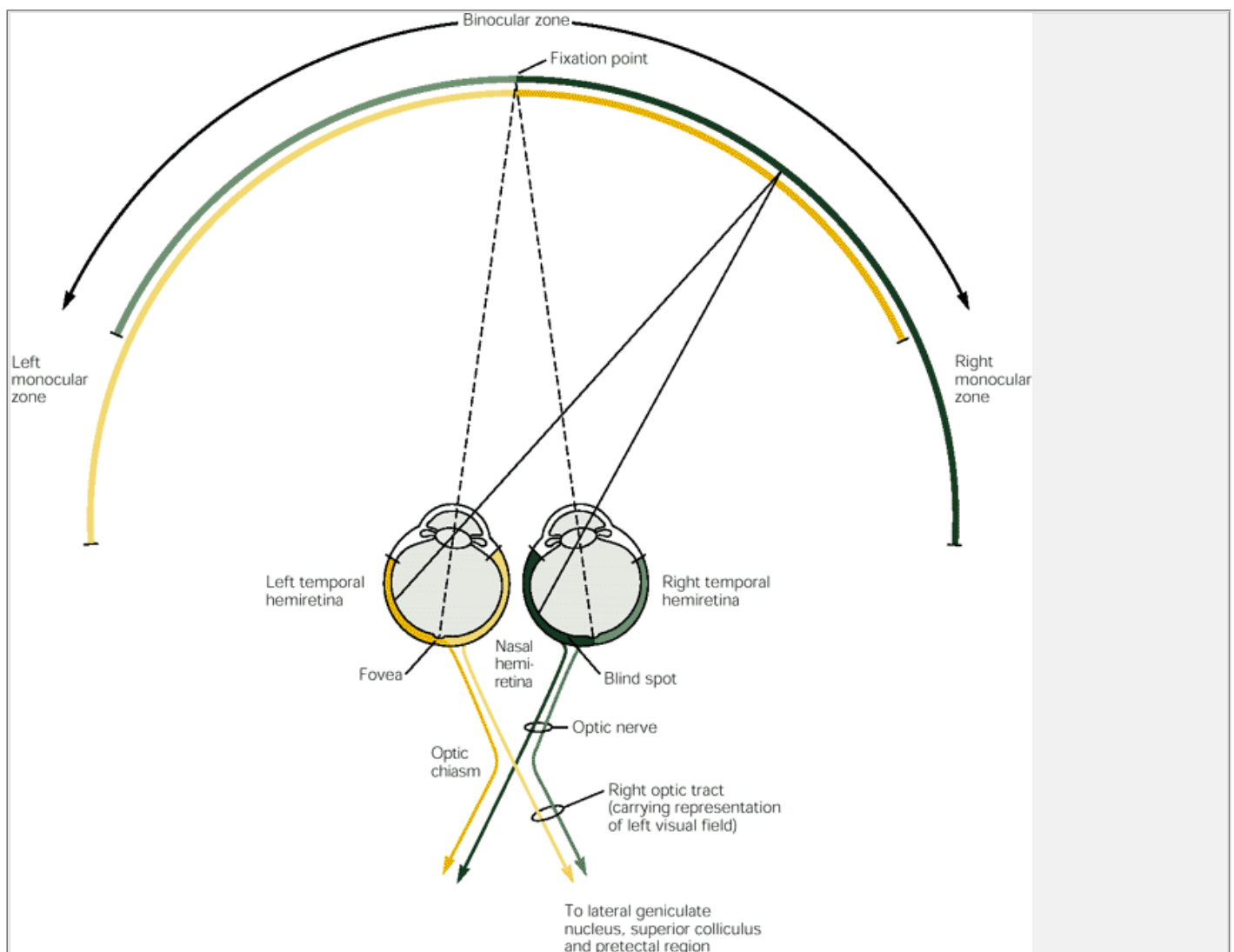


Figure 27-1 The visual field has both binocular and monocular zones. Light from the binocular zone strikes the retina in both eyes, whereas light from the monocular zone strikes the retina only in the eye on the same side. For example, light from a left monocular zone (temporal crescent) falls on only the ipsilateral nasal hemiretina and does not project upon the contralateral retina. The temporal and nasal hemiretinas are defined with respect to the fovea, the region in the center of the retina with highest acuity. The optic disc, the region where the ganglion cell axons leave the retina, is free of photoreceptors and therefore creates a gap, or blind spot, in the visual field for each eye (see [Figure 27-2](#)). While each optic nerve carries all the visual information from one eye, each optic tract carries a complete representation of one half of the binocular zone in the visual field. Fibers from the nasal hemiretina of each eye cross to the opposite side at the optic chiasm, whereas fibers from the temporal hemiretina do not cross. In the illustration, light from the right half of the binocular zone falls on the left temporal hemiretina and right nasal hemiretina. Axons from these hemiretinas thus contain a complete representation of the right hemifield of vision (see [Figure 27-6](#)).

The Retinal Image Is an Inversion of the Visual Field

For both clinical and experimental purposes it is important to distinguish between the retinal image and the visual field. The surface of the retina is divided with

respect to the midline: the *nasal hemiretina* lies medial to the fovea, the *temporal hemiretina* lateral to the fovea. Each half of the retina is further divided into dorsal (or superior) and ventral (or inferior) quadrants.

The visual field is the view seen by the two eyes without movement of the head. Left and right halves of
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the visual field can be defined when the foveas of both eyes are fixed on a single point in space. The *left visual hemifield* projects onto the nasal hemiretina of the left eye and the temporal hemiretina of the right eye. The *right visual hemifield* projects onto the nasal hemiretina of the right eye and the temporal hemiretina of the left eye (Figure 27-1). Light originating in the central region of the visual field, called the *binocular zone*, enters both eyes. In each half of the visual field there is also a *monocular zone*: light from the temporal portion of the visual hemifield projects onto only the nasal hemiretina of the eye on the same side (the ipsilateral nasal hemiretina). This monocular portion of the visual field is also called the *temporal crescent* because it constitutes the crescent-shaped temporal extreme of each visual field. Since there is no binocular overlap in this region, vision is lost in the entire temporal crescent if the nasal hemiretina is severely damaged.

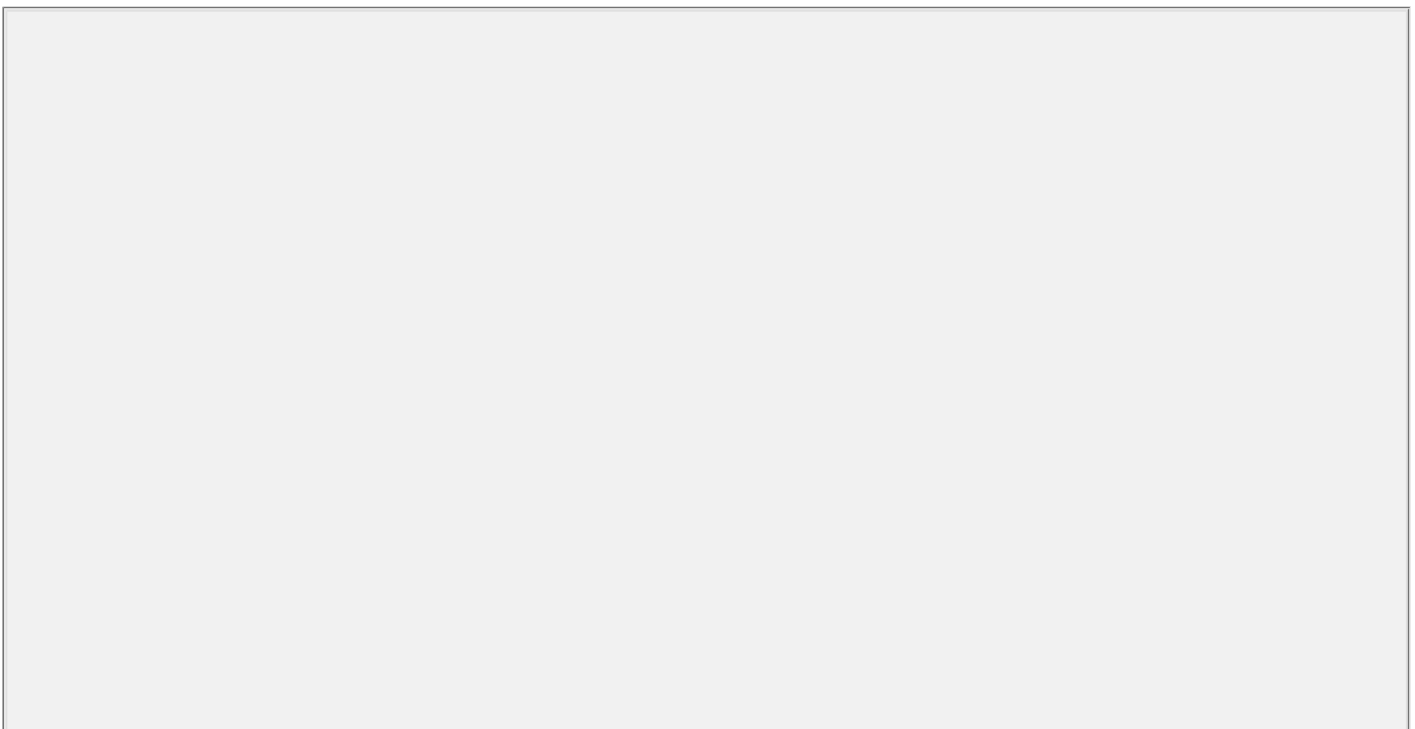


Figure 27-2 Locate the blind spot in your left eye by shutting the right eye and fixating the upper cross with the left eye. Hold the book about 15 inches from the eye and move it slightly nearer and farther from the eye until the circle on the left disappears. At this point the circle occupies the blind spot in the left eye. If you fixate the left eye on the lower cross, the gap in the black line falls on the blind spot and the black line is seen as continuous. (Adapted from Hurvich 1981.)

The region of the retina from which the ganglion cell axons exit, the optic disc, contains no photoreceptors and therefore is insensitive to light—a *blind spot* in the retina. Since the disc is nasal to the fovea in each eye (Figure 27-1), light coming from a single point in the binocular zone never falls on both blind spots simultaneously so that in normal vision we are unaware of them. We can experience the blind spot only by using one eye (Figure 27-2). The blind spot demonstrates what blind people experience—not blackness, but simply nothing. It also explains why damage to large regions of the peripheral retina goes unnoticed. In these instances no large dark zone appears in the periphery, and it is usually through accidents, such as bumping into an unnoticed object, or through clinical testing of the visual fields, that this absence of sight is noticed.

In tracing the flow of visual information to the brain we should keep in mind the correspondence between regions of the visual field and the retinal image. This relationship can be particularly difficult to follow for two reasons. First, the lens of the eye inverts the visual image (Figure 27-3). The upper half of the visual field projects onto the inferior (ventral) half of the retina, while the lower half of the visual field projects onto the superior (dorsal) half of the retina. Thus, damage to the inferior half of the retina of one eye causes a monocular deficit in the upper half of the visual field. Second, a single point in the binocular portion of one visual hemifield projects onto different regions of the two retinas. For example, a point of light in the binocular half of the right visual hemifield falls upon the temporal hemiretina of the left eye and the nasal hemiretina of the right eye (see Figure 27-1)

Axons from the ganglion cells in the retina extend through the optic disc and, at the optic chiasm, the fibers from the *nasal* half of each retina cross to the opposite side of the brain. The axons from ganglion cells in the temporal hemiretinas do not cross. Thus, the optic chiasm fibers from both retinas are bundled in the left and right optic tracts. In this arrangement the axons from the *left half of each retina* (the temporal hemiretina of the left eye and the nasal hemiretina of the right eye) project in the left optic tract, which thus carries a complete representation of the *right hemifield of vision* (Figure 27-1). Fibers from the *right half of each retina* (the nasal hemiretina of the left eye and the temporal hemiretina of the right eye) project in the right optic tract, which carries a complete representation of the *left hemifield of vision*. This separation of the right visual hemifield into the left optic tract and the left visual hemifield into the right optic tract is maintained in all the projections to the subcortical visual nuclei, which we consider next.



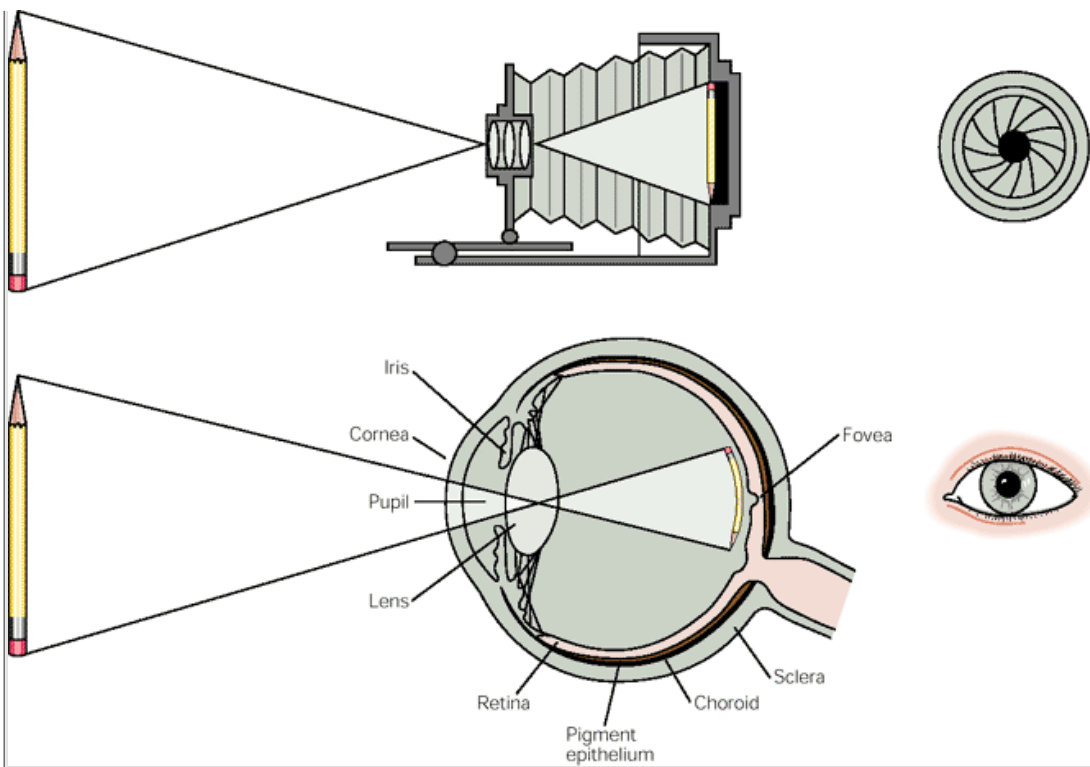


Figure 27-3 The lens of the eye projects an inverted image on the retina in the same way as a camera. (Adapted from [Groves and Schlesinger 1979](#).)

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The Retina Projects to Subcortical Regions in the Brain

The axons of all retinal ganglion cells stream toward the optic disc, where they become myelinated and together form the bilateral optic nerves. The optic nerves from each eye project to the optic chiasm, where fibers from each eye destined for one or the other side of the brain are sorted out and rebundled in the bilateral optic tracts, which project to three major subcortical targets: the pretectum, the superior colliculus, and the lateral geniculate nucleus ([Figure 27-4](#)). The following discussion of the details of these projections, and particularly our description of cellular activity along these pathways, is based on research in monkeys whose visual systems are similar to those of humans.

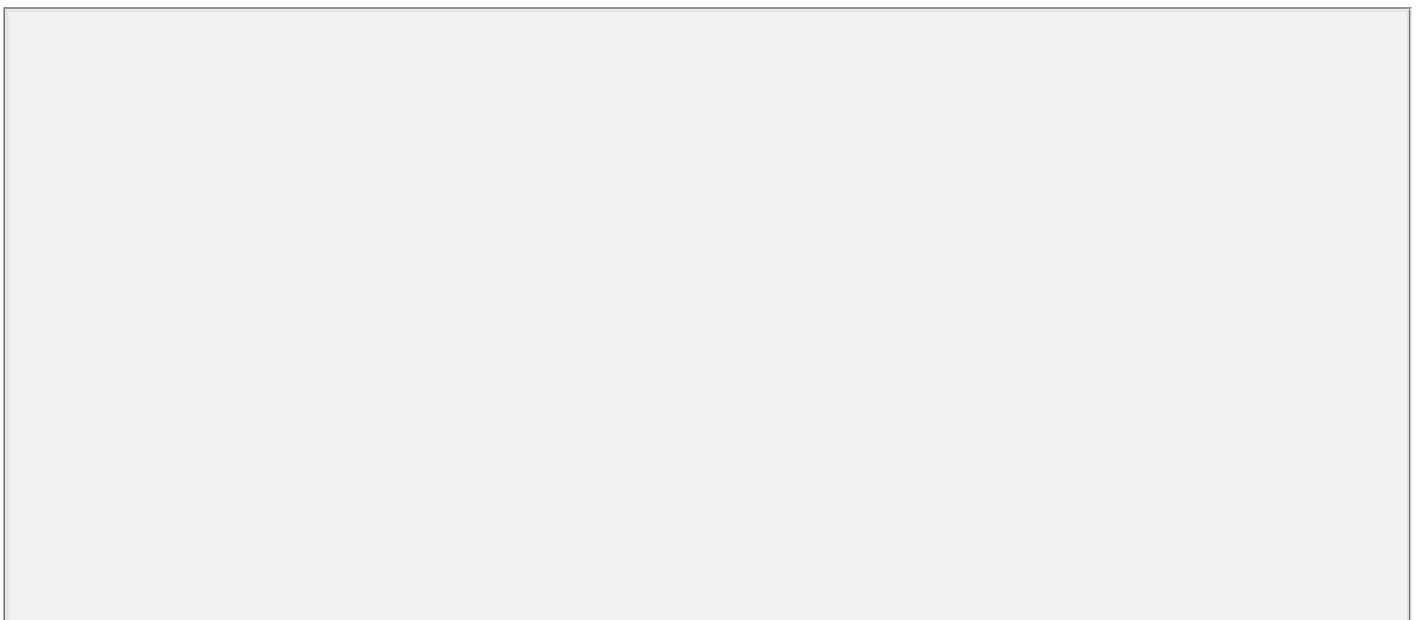
The Superior Colliculus Controls Saccadic Eye Movements

The superior colliculus is a structure of alternating gray cellular and white (axonal) layers lying on the roof of the midbrain. Retinal ganglion cells project directly to the superficial layers and form a map of the contralateral visual field. Cells in the superficial layers in turn project through the pulvinar nucleus of the thalamus to a broad area of the cerebral cortex, thus forming an indirect pathway from the retina to the cerebral cortex.

The superior colliculus also receives extensive cortical inputs. The superficial layers receive input from the visual cortex, while deeper layers receive projections from many other areas of the cerebral cortex. These deep layers have the same map of the visual field found in the superficial layers, but the cells also respond to auditory and somatosensory stimuli as well. The locations in space represented by these multisensory inputs are aligned with one another. For example, neurons that respond to a bird flying within the contralateral visual field also will respond to its singing when it is in that same part of the field. In this way, different types of sensory information about an object are conveyed to a common region of the superior colliculus. The auditory and somatosensory inputs are adjusted to fit with the visual map in situations where the maps of these other modalities might diverge. An example of such divergence occurs when our eyes are directed to one side but our head

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is directed straight ahead (with respect to the body); a bird sitting where we are looking will fall in the center of the visual field but its song will locate it to one side of the auditory field.



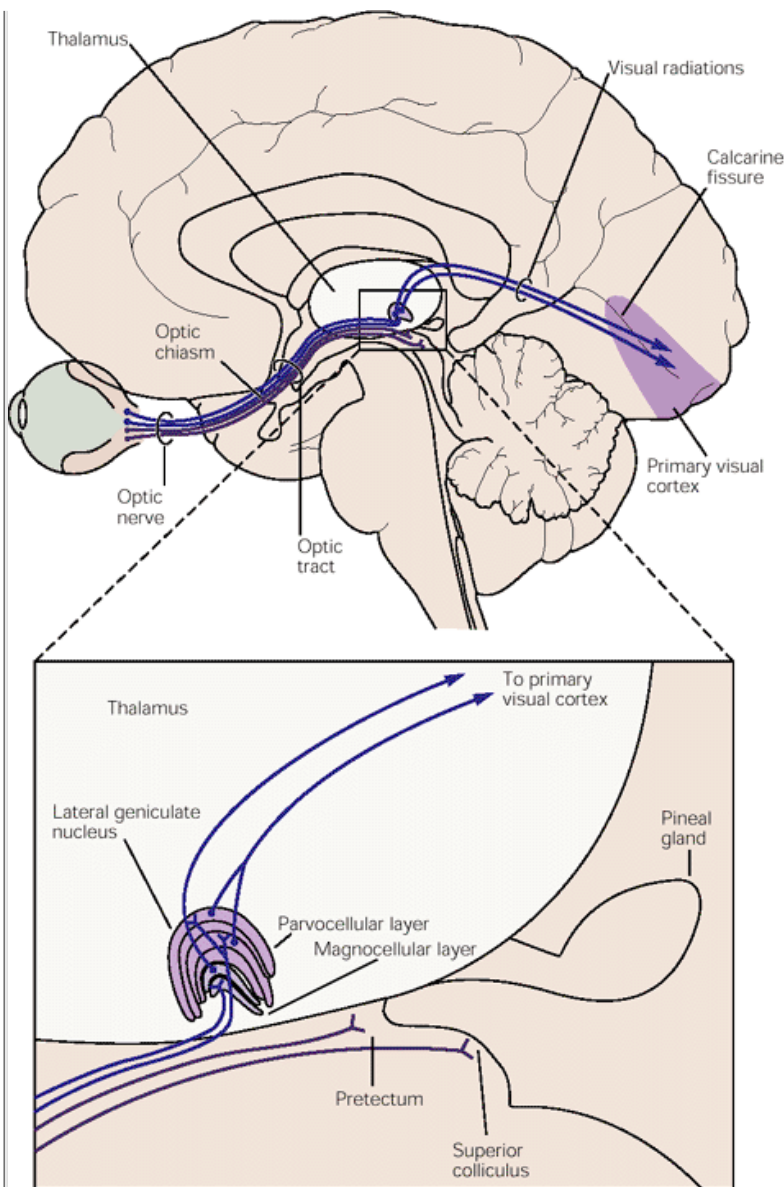


Figure 27-4 A simplified diagram of the projections from the retina to the visual areas of the thalamus (lateral geniculate nucleus) and midbrain (pretectum and superior colliculus). The retinal projection to the pretectal area is important for pupillary reflexes, and the projection to the superior colliculus contributes to visually guided eye movements. The projection to the lateral geniculate nucleus, and from there to the visual cortex, processes visual information for perception.

Many cells lying in the deeper layers of the colliculus also discharge vigorously before the onset of saccadic eye movements, those movements that shift the gaze rapidly from one point in the visual scene to another. These cells form a movement map in the intermediate layers of the colliculus, and this map is in register with the visual map: Cells responding to stimuli in the left visual field will discharge vigorously before a leftward-directed saccade. Although the superior colliculus receives direct retinal input, the control of these saccadic eye movements is thought to be determined more by the inputs from the cerebral cortex that reach the intermediate layers. The organization within the brain of this system for generating saccadic eye movements is considered in [Chapter 39](#).

The Pretectum of the Midbrain Controls Pupillary Reflexes

Light shining in one eye causes constriction of the pupil in that eye (the direct response) as well as in the other eye (the consensual response). Pupillary light reflexes are mediated by retinal ganglion cells that project to the pretectal area of the midbrain, just rostral to the superior

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colliculus where the midbrain fuses with the thalamus. The cells in the pretectal area project bilaterally to preganglionic parasympathetic neurons in the Edinger-Westphal (or accessory oculomotor) nucleus, which lies immediately adjacent to the neurons of the oculomotor (cranial nerve III) nucleus ([Figure 27-5](#)). Preganglionic neurons in the Edinger-Westphal nucleus send axons out of the brain stem in the oculomotor nerve to innervate the ciliary ganglion. This ganglion contains the postganglionic neurons that innervate the smooth muscle of the pupillary sphincter that constricts the pupil. A sympathetic pathway innervates the pupillary radial iris muscles that dilate the pupils.

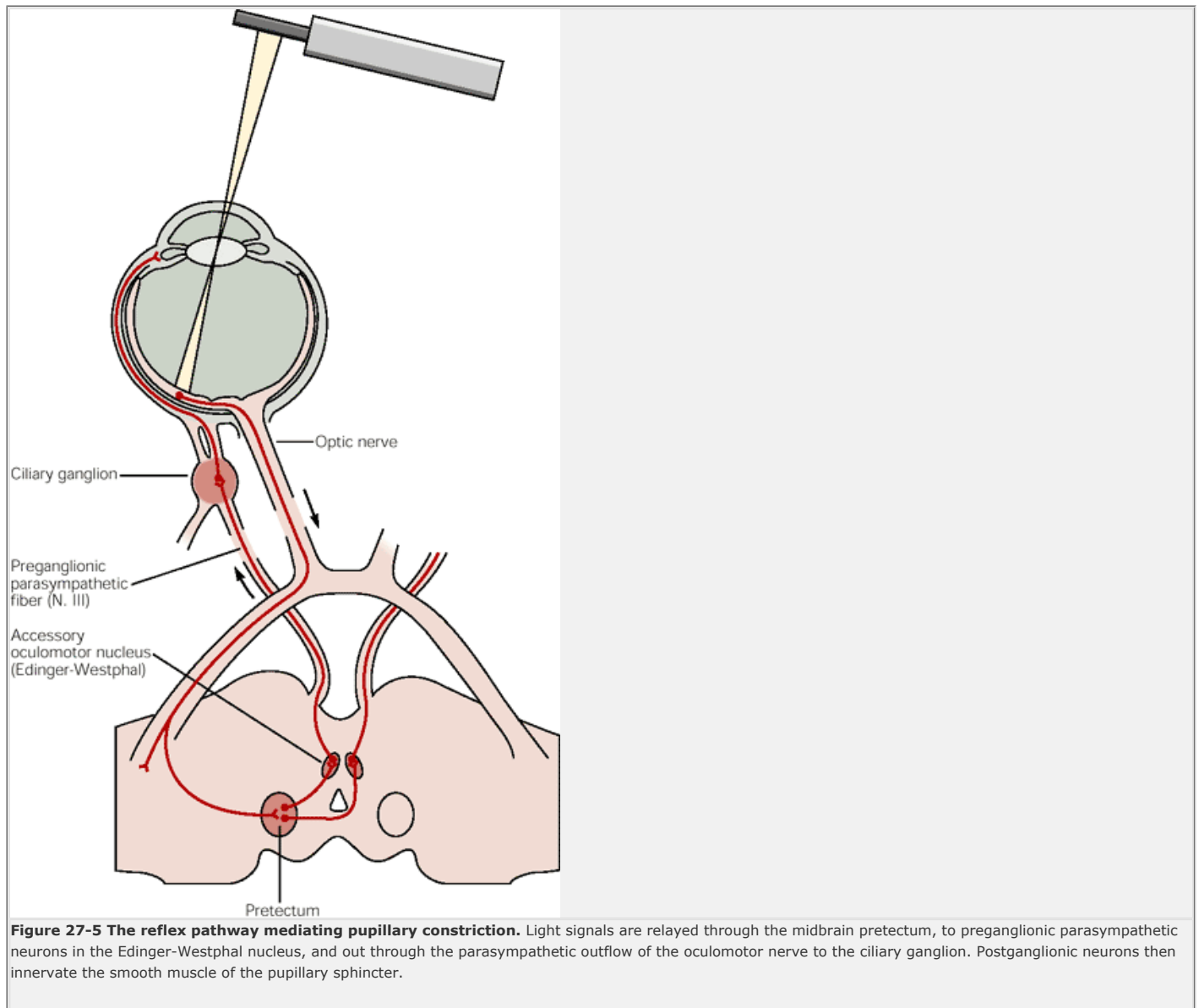
Pupillary reflexes are clinically important because they indicate the functional state of the afferent and efferent pathways mediating them. As an example, if light directed to the left eye of a patient elicits a consensual response in the right eye but not a direct one in the left eye, then the afferent limb of the reflex, the optic nerve, is intact but the efferent limb to the left eye is damaged, possibly by a lesion of the oculomotor nerve. In contrast, if the afferent optic nerve is lesioned unilaterally, illumination of the affected eye will cause no change in either pupil, but illumination of the *normal* eye will elicit both direct and consensual responses in the two eyes. The absence of pupillary reflexes in an unconscious patient is a symptom of damage to the midbrain, the region from which the oculomotor nerves originate.

The Lateral Geniculate Nucleus Is the Main Terminus for Input to the Visual Cortex

Ninety percent of the retinal axons terminate in the lateral geniculate nucleus, the principal subcortical structure that carries visual information to the cerebral cortex. Without this pathway visual perception is lost, although some very limited stimulus detection and movement toward objects in the visual field still is possible. This residual vision, possibly mediated by the visual pathway passing through the superior colliculus, has been called *blindsight*.

Ganglion cells in the retina project in an orderly manner to points in the lateral geniculate nucleus, so that in each lateral geniculate nucleus there is a retinotopic

representation of the contralateral half of the visual field. As in the somatosensory system, all areas of the retina are not represented equally in the nucleus. The fovea, the area of the retina with the highest density of ganglion cells, has a relatively larger representation than does the periphery of the retina. About half of the neural mass in the lateral geniculate nucleus (and in the primary visual cortex) represents the fovea and the region just around it. The much larger peripheral portions of the retina, with the lowest density of ganglion cells, are less well represented.



The retinal ganglion cells in and near the centrally located fovea are densely packed to compensate for the fact that the retina's central area is less than its periphery (due to the concavity of the retina). Since this physical limitation does not exist beyond the retina, neurons in the lateral geniculate nucleus and primary visual cortex are fairly evenly distributed—connections from the more numerous neurons in the fovea are distributed

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over a wide area. The ratio of the area in the lateral geniculate nucleus (or in the primary visual cortex) to the area in the retina representing one degree of the visual field is called the *magnification factor*.

In primates, including humans, the lateral geniculate nucleus contains six layers of cell bodies separated by intralaminar layers of axons and dendrites. The layers are numbered from 1 to 6, ventral to dorsal (Figure 27-6). Axons of the M and P retinal ganglion cells described in Chapter 26 remain segregated in the lateral geniculate nucleus. The two most ventral layers of the nucleus contain relatively large cells and are known as the *magnocellular layers*; their main retinal input is from M ganglion cells. The four dorsal layers are known as *parvocellular layers* and receive input from P ganglion cells. Both the magnocellular and parvocellular layers include on- and off-center cells, just as there are on- and off-center ganglion cells in the retina.

An individual layer in the nucleus receives input from one eye only: fibers from the contralateral nasal hemiretina contact layers 1, 4, and 6; fibers from the ipsilateral temporal hemiretina contact layers 2, 3, and 5 (Figure 27-6). Thus, although one lateral geniculate nucleus carries complete information about the contralateral visual field, the inputs from each eye remain segregated. The inputs from the nasal hemiretina of the contralateral eye represent the complete contralateral visual hemifield, whereas the inputs from the temporal hemiretina of the ipsilateral eye represent only 90% of the hemifield because they do not include the temporal crescent (see Figure 27-1)

Retinal ganglion cells have concentric receptive fields, with an antagonistic center-surround organization that allows them to measure the contrast in light intensity between their receptive field center and the surround (see Chapter 26). Do the receptive fields of lateral geniculate neurons have a similar organization? David Hubel and Torsten Wiesel, who first addressed this question in the early 1960s, found that they did. They directed light onto the retina of cats and monkeys by projecting patterns of light onto a screen in front of the animal. They found that receptive fields of neurons in the lateral geniculate nucleus are similar to those in the retina: small concentric fields about one degree in diameter. As in the retina, the cells are either on-center or off-center. Like the retinal ganglion cells, cells in the lateral geniculate nucleus respond best to small spots of light in the center of their receptive field. Diffuse illumination of the whole receptive field produces only weak responses. This similarity in the receptive properties of cells in the lateral geniculate nucleus and retinal ganglion cells derives in part from the fact that each geniculate neuron receives its main retinal input from only a very few ganglion cell axons.

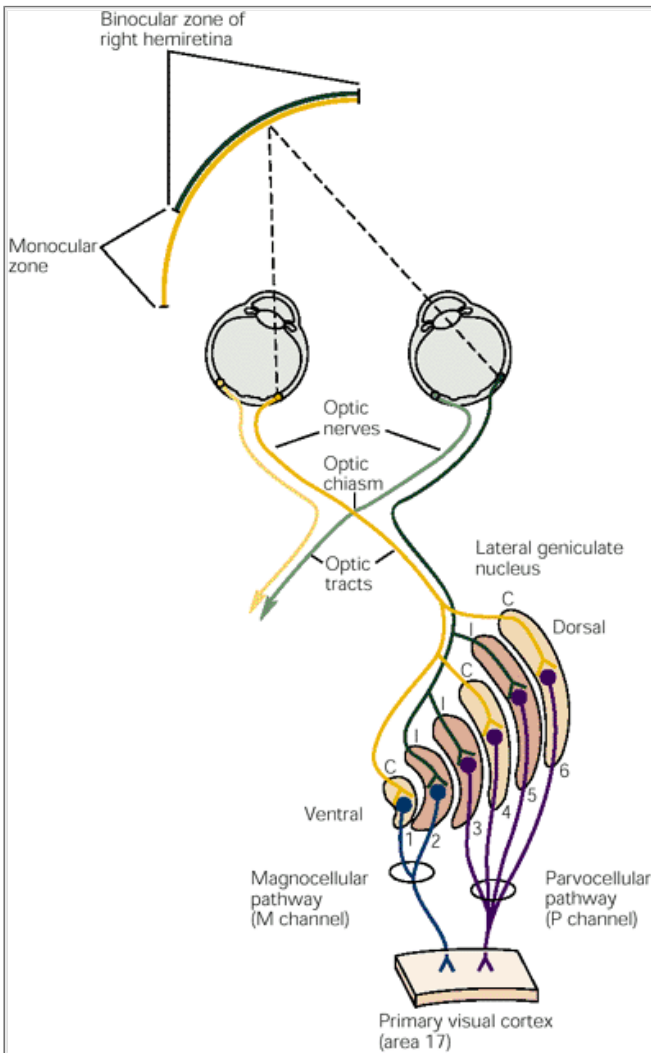


Figure 27-6 The lateral geniculate nucleus is the principal subcortical site for processing visual information. Inputs from the right hemiretina of each eye project to different layers of the right lateral geniculate nucleus to create a complete representation of the left visual hemifield. Similarly, fibers from the left hemiretina of each eye project to the left lateral geniculate nucleus (not shown). The temporal crescent is not represented in contralateral inputs (see [Figure 27-1](#)). Layers 1 and 2 comprise the magnocellular layers; layers 3 through 6 comprise the parvocellular layers. All of these project to area 17, the primary visual cortex. (C = contralateral input; I = ipsilateral input.)

Magnocellular and Parvocellular Pathways Convey Different Information to the Visual Cortex

We have already seen that the M ganglion cells of the retina project to the magnocellular layers of the lateral geniculate nucleus and that the P ganglion cells project

to the parvocellular layers. The parvocellular and magnocellular layers in turn project to separate layers of the primary visual cortex as we shall see later in this chapter. This striking anatomical segregation has led to the view that these separate sequences of retinal ganglion, lateral geniculate, and visual cortical cells can be regarded as two parallel pathways, referred to as the M and P pathways.

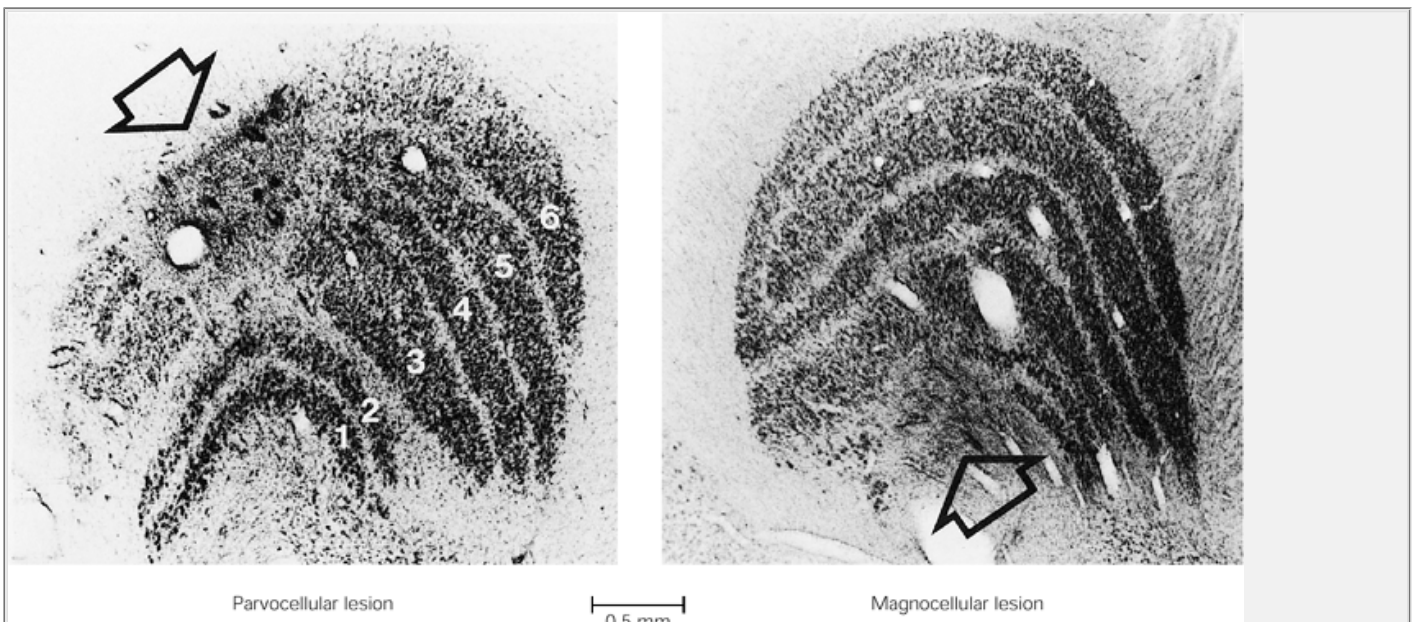


Figure 27-7 Samples of lesions (arrows) in the lateral geniculate nucleus of the monkey that selectively alter visual function. In the photograph on the left the geniculate layers are numbered. Lesions were made with an excitotoxin (ibotenic acid). Coronal sections were stained with cresyl violet. (From Schiller et al. 1990.)

As indicated in Table 27-1, there are striking differences between cells in the M and P pathways. The most prominent difference between the cells in the lateral geniculate nucleus is their sensitivity to *color contrast*. The P cells respond to changes in color (red/green and blue/yellow) regardless of the relative brightness of the colors, whereas M cells respond weakly to changes of color when the brightness of the color is matched.

Table 27-1 Differences in the Sensitivity of M and P Cells to Stimulus Features

Stimulus feature	Sensitivity	
	M cells	P cells
Color contrast	No	Yes
Luminance contrast	Higher	Lower
Spatial frequency	Lower	Higher
Temporal frequency	Higher	Lower

Luminance contrast is a measure of the difference between the brightest and darkest parts of the stimulus—M cells respond when contrast is as low as 2%, whereas P cells rarely respond to contrasts less than 10%. The M and P cells also differ in their response to spatial and temporal frequency. *Spatial frequency* is the number of repetitions of a pattern over a given distance. For example, alternating light and dark bars each occurring 10 times over a visual angle of one degree have a spatial frequency of 10 cycles per degree. *Temporal frequency* is how rapidly the pattern changes over time; turning the bars of a grating on and off 10 times per second would produce a temporal frequency of 10 Hz. The M cells tend to have lower spatial resolution and higher temporal resolution than P cells.

One way to explore further the contribution of the M and P pathways is by selectively removing one or the other in a monkey and then measuring the monkey's ability to perform a task that is thought to depend on the ablated pathway. Because the M and P cells are in different layers in the lateral geniculate nucleus, removal of a pathway is possible through localized chemical lesions (Figure 27-7).

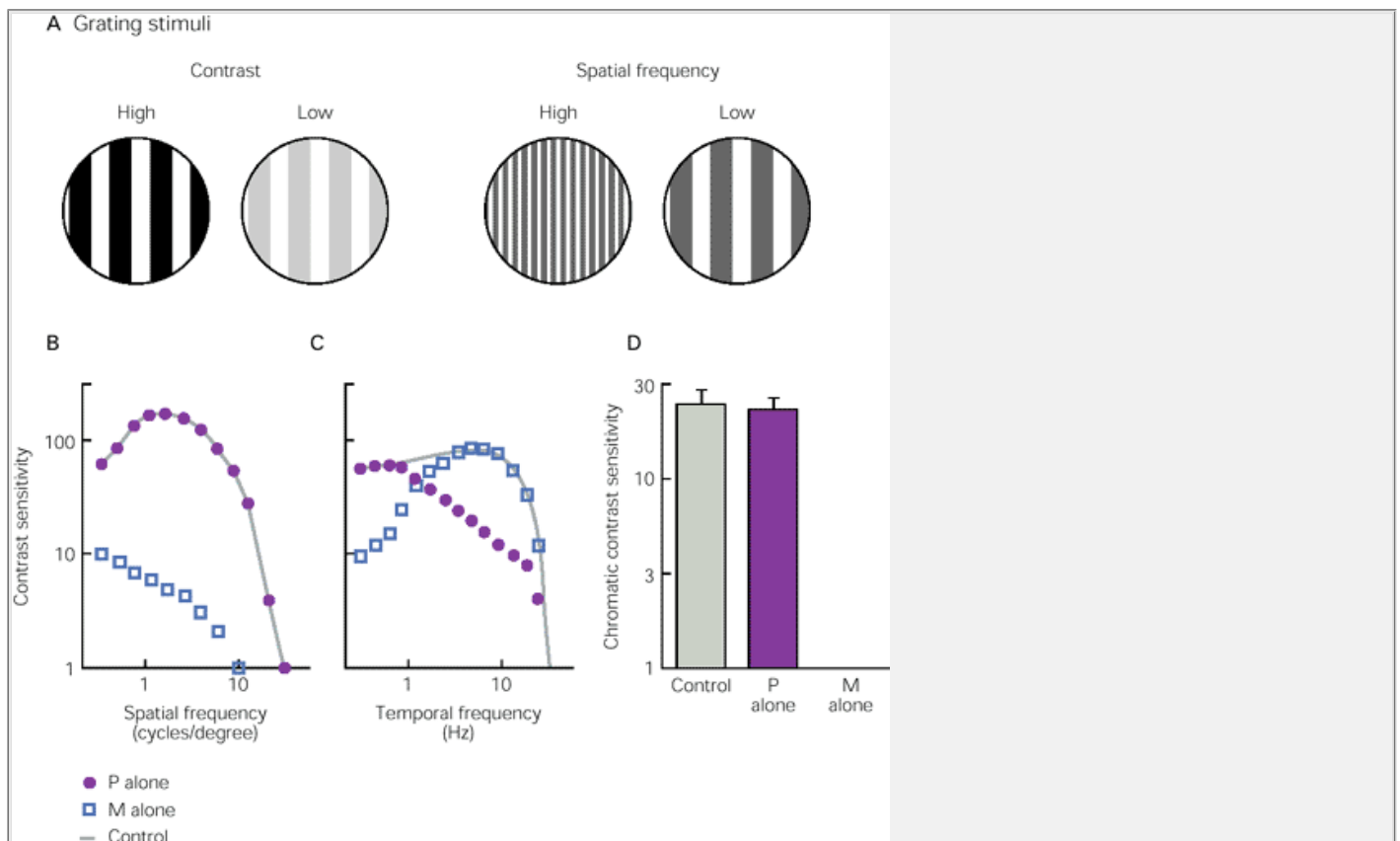


Figure 27-8 Visual losses after selective lesioning of the magnocellular and parvocellular layers of the lateral geniculate nucleus in monkeys. The monkeys were trained to look at a fixation spot on a TV monitor and then grating stimuli were presented at one location in the visual field. The location was selected to coincide with the part of the visual field affected by a lesion in the lateral geniculate nucleus (such as those shown in Figure 27-7). Each lesion was centered on one layer that received information from one eye, so in the test the eye unaffected by the lesion was covered. On each presentation the monkeys indicated whether the gratings were vertical or horizontal, and this distinction became more difficult as the luminance contrast of the gratings became very low or the spatial frequency became very high.

A. Luminance contrast is the difference between the brightest and darkest parts of the grating. Spatial frequency is the number of light and dark bars (cycles) in the grating per degree of visual angle. Temporal frequency (not shown) is how fast the stationary grating is turned on and off per second (Hz).

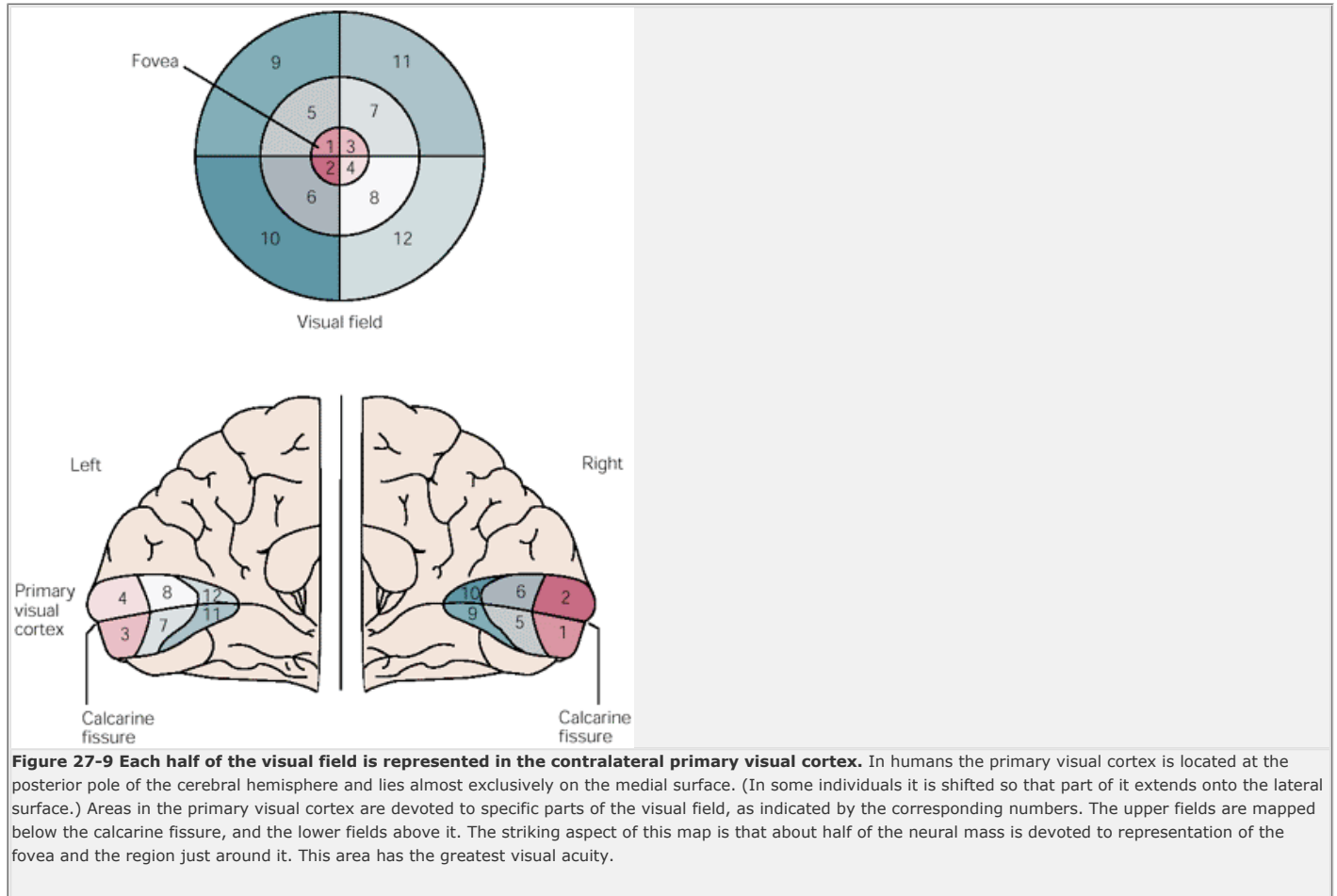
B. Contrast sensitivity is the inverse of the lowest stimulus contrast that can be detected. Contrast sensitivity for all spatial frequencies is reduced when only the magnocellular (M) pathway remains after parvocellular (P) lesion. The solid blue line in B and C shows sensitivity of the normal monkey; **filled circles** show the contribution of the P pathway (after M lesions) and **open squares** the contribution of the M pathway (after P lesions).

C. Contrast sensitivity to a grating with low spatial frequency is reduced at lower temporal frequencies when only M cells remain and at higher frequencies when only P cells remain.

D. Color contrast is measured the same way as luminance contrast except that bars of different colors were used instead of light and dark bars. Color contrast sensitivity is lost when only the M cells remain. (Adapted from [Merigan and Maunsell 1993](#).)

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The effects of these focal lesions on color vision are striking. Removal of P cells (leaving M cells alone) leads to a complete loss of color vision ([Figure 27-8D](#)), a result explained by the color sensitivity of these cells. Lesions in the M cell layers (leaving P cells alone) do not produce such deficits, consistent with the lack of color sensitivity in these cells. Selective lesions of M cells make it difficult for monkeys to perceive a pattern of bright and dark bars that have both low spatial frequency (more widely spaced bars) and high temporal frequency (bars turned on and off at higher rates). To make the discriminations, the luminance contrast of the bright and dark bars must be higher than for normal monkeys ([Figure 27-8B, C](#)). Lesions in the P cell layers produce the opposite effect—they make it difficult for the monkey to discriminate between stimuli that have both high spatial frequency (more closely spaced bars) and low temporal frequency (bars turned on and off at lower rates).



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Thus both the response properties of single cells and the behavioral consequence of removing the cells show that the M and P cells make different contributions to perception. The P cells are critical for color vision and are most important for vision that requires high spatial and low temporal resolution vision. The M cells contribute most to vision requiring low spatial and high temporal resolution. Such specialization of processing is critical for the elemental properties of vision such as spatial and temporal resolution and color vision.

Although we know a great deal about the cell types and circuitry of the lateral geniculate nucleus, and about the information conveyed by the P and M cells, the function of the nucleus is not yet clear. In fact, only 10-20% of the presynaptic connections onto geniculate relay cells come from the retina! The majority of inputs come from other regions, and many of these, particularly those from the reticular formation in the brain stem and from the cortex, are feedback inputs. This input to the lateral geniculate nucleus may control the flow of information from the retina to the cortex.

The Primary Visual Cortex Organizes Simple Retinal Inputs Into the Building Blocks of Visual Images

The first point in the visual pathway where the receptive fields of cells are significantly different from those of cells in the retina is the primary visual cortex, also called visual area 1 (abbreviated V1). This region of cortex, Brodmann's area 17, is also called the *striate cortex* because it contains a prominent stripe of white matter in layer 4, the *stria of Gennari*, consisting of myelinated axons. Like the lateral geniculate nucleus and superior colliculus, the primary visual cortex in each cerebral hemisphere receives information exclusively from the contralateral half of the visual field ([Figure 27-9](#)).

The primary visual cortex in humans is about 2 mm thick and consists of six layers of cells (layers 1-6) between the pial surface and the underlying white matter. The principal layer for inputs from the lateral geniculate nucleus is layer 4, which is further subdivided into four sublayers (sublaminae): 4A, 4B, 4C α , and 4C β . Tracings of resident cells and axonal inputs in the monkey have shown that the M and P cells of the lateral geniculate nucleus terminate in different layers and even in different sublayers. The axons of M cells terminate principally in sublamina 4C α ; the axons of most P cells terminate principally in sublamina 4C β ([Figure 27-10A](#)). Thus, the segregation of the parvocellular and magnocellular pathways continues to be maintained at this level of processing.

Axons from a third group of cells, located in the intralaminar region of the lateral geniculate nucleus, terminate in layers 2 and 3, where they innervate patches of cells called *blobs*, a functional grouping that we shall discuss below. These intralaminar cells probably receive their retinal inputs primarily from ganglion cells other than those providing inputs to the M and P cells. These cells might therefore represent another pathway in parallel to the P and M pathways from the retina to the visual cortex, but little is now known about their function.

As we have seen in [Chapter 17](#), the cortex contains two basic classes of cells. *Pyramidal cells* are large and have long spiny dendrites; they are projection neurons whose axons project to other brain regions as well as

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interconnecting neurons in local areas. *Nonpyramidal cells* are small and stellate in shape and have dendrites that are either spiny (spiny stellate cells) or smooth (smooth stellates). They are local interneurons whose axons are confined to the primary visual cortex ([Figure 27-10B](#)). The pyramidal and spiny stellate cells are excitatory and many use glutamate or aspartate as their transmitters; the smooth stellate cells are inhibitory and many contain γ -aminobutyric acid (GABA).

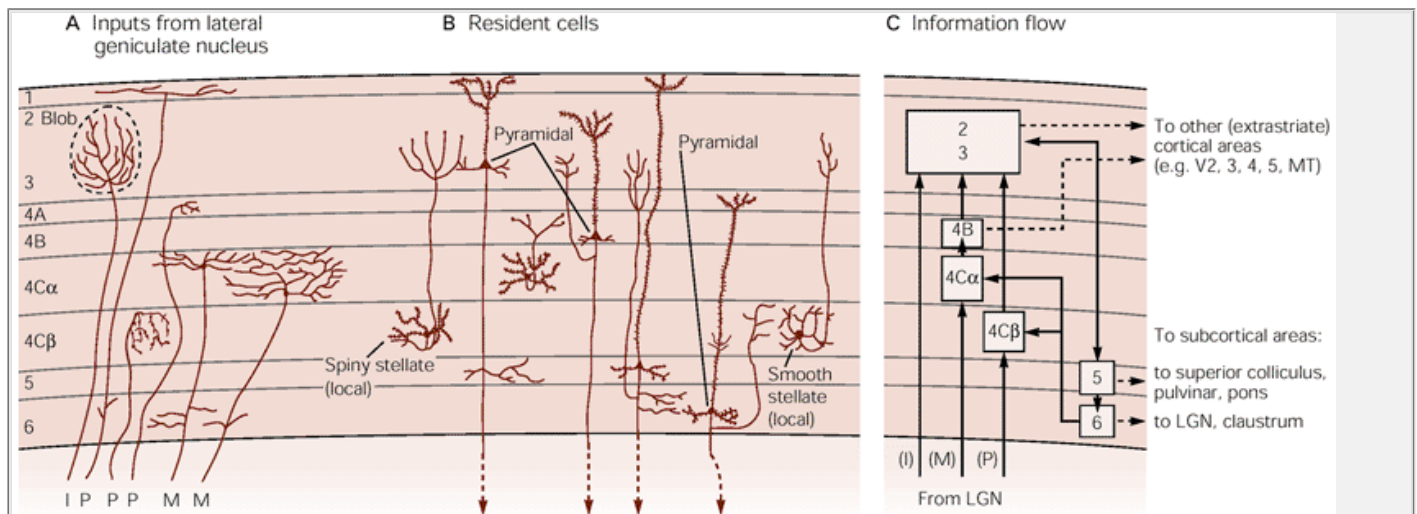


Figure 27-10 The primary visual cortex has distinct anatomical layers, each with characteristic synaptic connections. (Adapted from [Lund 1988](#).)

A. Most afferent fibers from the lateral geniculate nucleus terminate in layer 4. The axons of cells in the parvocellular layers (**P**) terminate primarily in layer 4C β , with minor inputs to 4A and 1, while the axons of cells in the magnocellular layers (**M**) terminate primarily in layer 4C α . Collaterals of both types of cells also terminate in layer 6. Cells of the intralaminar regions (**I**) of the lateral geniculate nucleus terminate in the blob regions of layers 2 and 3.

B. Several types of neurons make up the primary visual cortex. Spiny stellate and pyramidal cells, both of which have spiny dendrites, are excitatory. Smooth stellate cells are inhibitory. Pyramidal cells project out of the cortex, whereas both types of stellate cells are local neurons.

C. Conception of information flow based on anatomical connections. (**LGN** = lateral geniculate nucleus; **MT** = middle temporal area.)

Inputs. Axons from M and P cells in the lateral geniculate nucleus end on spiny stellate cells in the sublayers of 4C, and these cells project axons to layer 4B or the upper layers 2 and 3. Axons from cells in the intralaminar zones of the lateral geniculate nucleus project directly to layers 2 and 3.

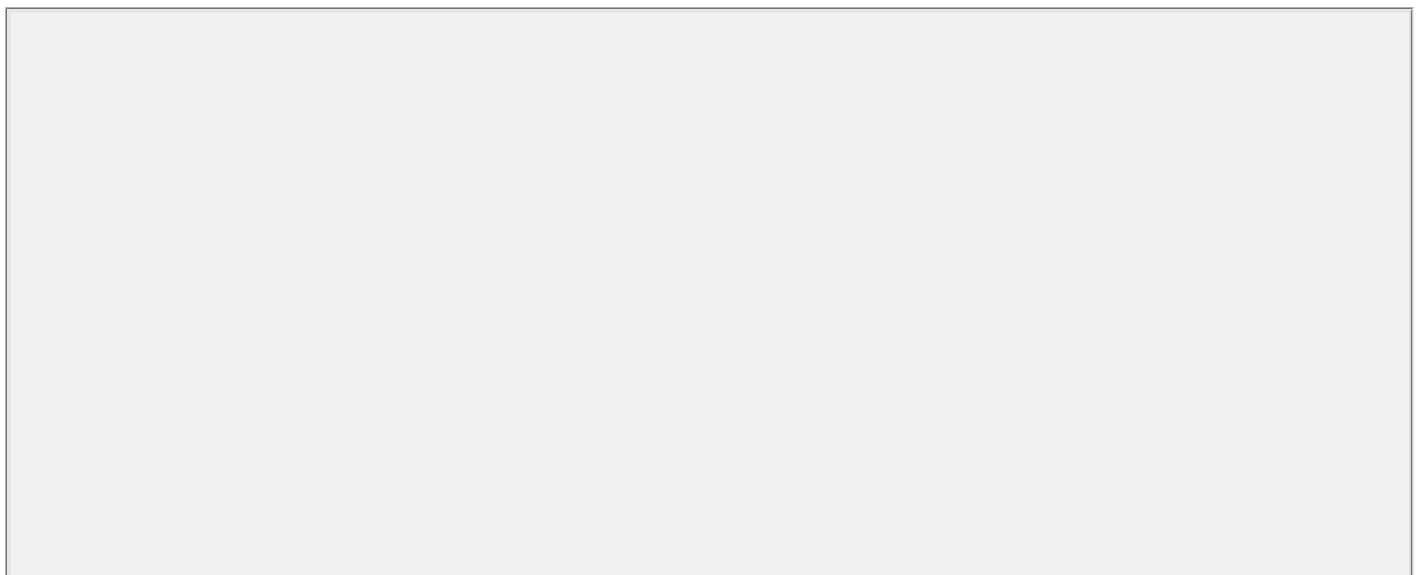
Intracortical connections. Axon collaterals of pyramidal cells in layers 2 and 3 project to layer 5 pyramidal cells, whose axon collaterals project both to layer 6 pyramidal cells and back to cells in layers 2 and 3. Axon collaterals of layer 6 pyramidal cells then make a loop back to layer 4C onto smooth stellate cells.

Output. Each layer, except for 4C, has outputs for V1 and each is different. The cells in layers 2, 3, and 4B project to extrastriate visual cortical areas. Cells in layer 5 project to the superior colliculus, the pons, and the pulvinar. Cells in layer 6 project back to the lateral geniculate nucleus and the claustrum.

Once afferents from the lateral geniculate nucleus enter the primary visual cortex, information flows systematically from one cortical layer to another, starting with the spiny stellate cells, which predominate in layer 4. The spiny stellate cells distribute the input from the lateral geniculate nucleus to the cortex and the pyramidal cells feed axon collaterals upward and downward to integrate activity within the layers of V1 ([Figure 27-10C](#)).

Simple and Complex Cells Decompose the Outlines of a Visual Image Into Short Line Segments of Various Orientations

How is the complexity of the circuitry in the cerebral cortex reflected in the response properties of cortical cells? Hubel, Wiesel, and their colleagues found that most cells above and below layer 4 respond optimally to stimuli that are substantially more complex than those that excite cells in the retina and lateral geniculate nucleus. Their most unexpected finding was that small spots of light—which are so effective in the retina, lateral geniculate nucleus, and in the input layer of the cortex 4C—are much less effective in all other layers of the visual cortex except possibly the blob regions in the superficial layers. Instead, cells respond best to stimuli that have linear properties, such as a line or bar. These cells belong to two major groups, simple and complex.



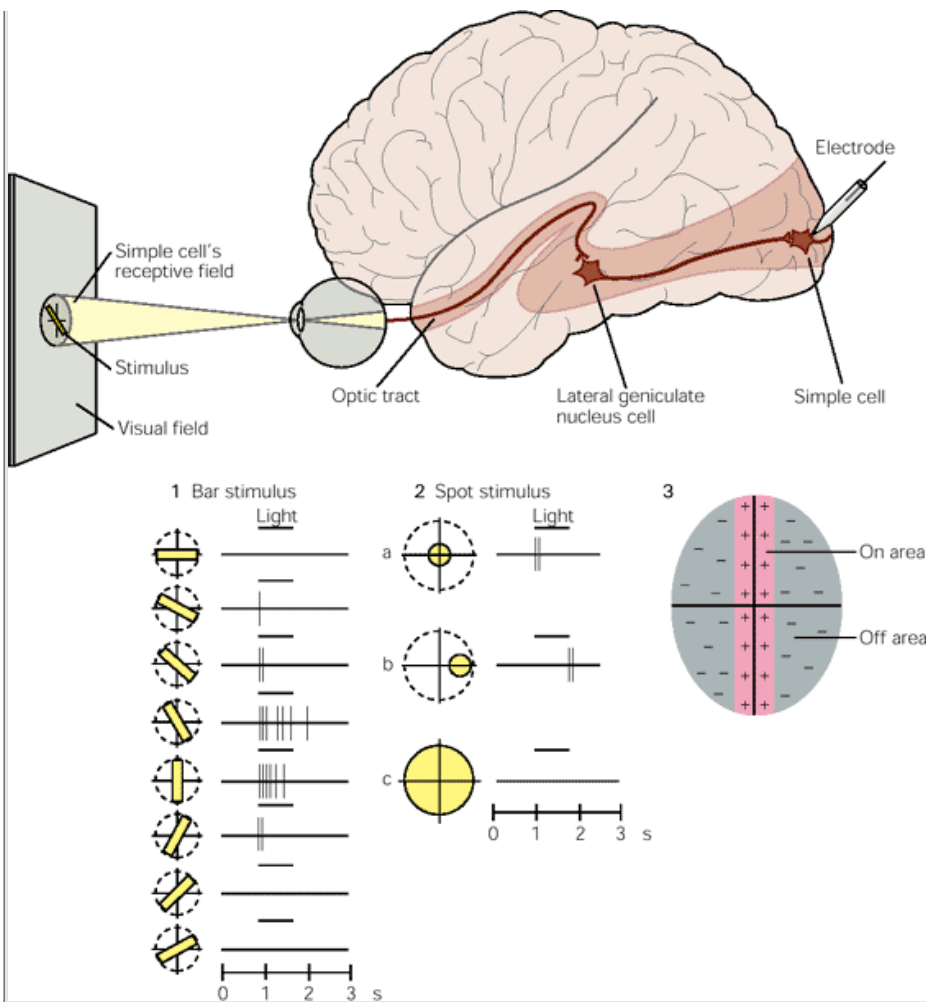


Figure 27-11 Receptive field of a simple cell in the primary visual cortex. The receptive field of a cell in the visual system is determined by recording activity in the cell while spots and bars of light are projected onto the visual field at an appropriate distance from the fovea. The records shown here are for a single cell. Duration of illumination is indicated by a line above each record of action potentials. (Adapted from [Hubel and Wiesel 1959](#) and [Zeki 1993](#).)

1. The cell's response to a bar of light is strongest if the bar of light is vertically oriented in the center of its receptive field.
2. Spots of light consistently elicit weak responses or no response. A small spot in the excitatory center of the field elicits only a weak excitatory response (a). A small spot in the inhibitory area elicits a weak inhibitory response (b). Diffuse light produces no response (c).
3. By using spots of light, the excitatory or "on" areas (+) and inhibitory or "off" areas (-) can be mapped. The map of the responses reveals an elongated "on" area and a surrounding "off" area, consistent with the optimal response of the cell to a vertical bar of light.

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The *simple* cells respond best to a bar of light with a specific orientation. For example, a cell that responds best to a vertical bar will not respond, or respond only weakly, to a bar that is horizontal or even oblique ([Figure 27-11](#)). Thus, an array of cells in the cortex, all receiving impulses from the same point on the retina but with rectilinear receptive fields with different axes of orientation, is able to represent every axis of rotation for that point on the retina.

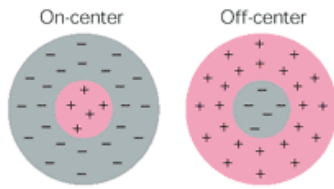
Simple cells also have excitatory and inhibitory zones in their receptive fields, although these zones are slightly larger than those for lateral geniculate cells ([Figure 27-12A, B](#)). For example, a cell may have a rectilinear excitatory zone (with its long axis running from 12 to 6 o'clock such as in [Figure 27-12B](#) upper right). For a cell with such a field, an effective stimulus must excite the specific segment of the retina innervated by receptors in the excitatory zone *and* have the correct linear properties (in this case an edge) *and* have a specific axis of orientation (in this case vertical, running from 12 to 6 o'clock).

Rectilinear receptive fields could be built up from many circular fields if the presynaptic connections from

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the lateral geniculate nucleus were appropriately arrayed on the simple cell ([Figure 27-12C](#)). Indeed, experiments have indicated that the excitatory ("on") regions in the receptive field of simple cells largely represent the input from on-center lateral geniculate cells while the inhibitory ("off") regions represent inputs from off-center lateral geniculate cells.

A Receptive fields of concentric cells of retina and lateral geniculate nucleus



B Receptive fields of simple cells of primary visual cortex

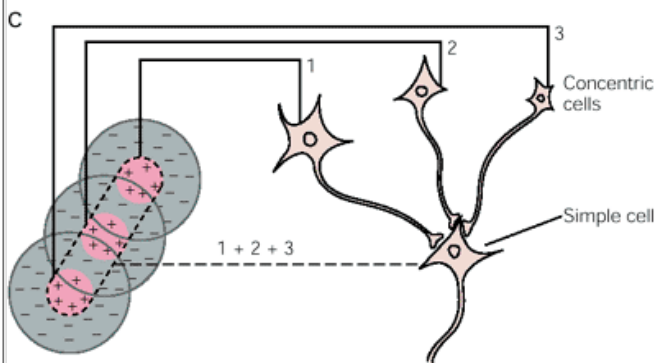
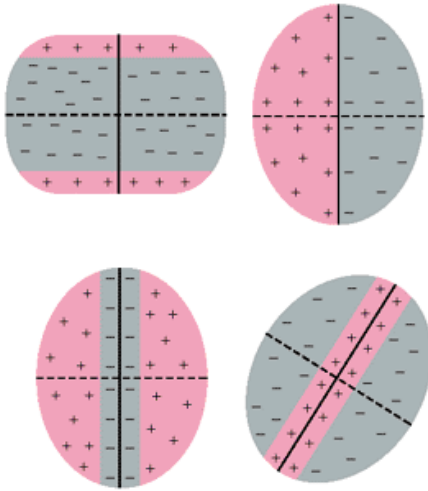


Figure 27-12 The receptive fields of simple cells in the primary visual cortex are different and more varied than those of the neurons in the retina and lateral geniculate nucleus.

A. Cells of the retina and lateral geniculate nucleus fall into two classes: on-center and off-center. The receptive fields of these neurons have a center-surround organization due to antagonistic excitatory (+) and inhibitory (-) regions.

B. The receptive fields of simple cells in the primary visual cortex have narrow elongated zones with either excitatory (+) or inhibitory (-) flanking areas. Despite the variety, the receptive fields of simple cells share three features: (1) specific retinal position, (2) discrete excitatory and inhibitory zones, and (3) a specific axis of orientation.

C. Model of the organization of inputs in the receptive field of simple cells proposed by Hubel and Wiesel. According to this model, a simple cortical neuron in the primary visual cortex receives convergent excitatory connections from three or more on-center cells that together represent light falling along a straight line in the retina. As a result, the receptive field of the simple cortical cell has an elongated excitatory region, indicated by the colored outline in the receptive field diagram. The inhibitory surround of the simple cortical cells is probably provided by off-center cells whose receptive fields (not shown) are adjacent to those of the on-center cells. (Adapted from [Hubel and Wiesel 1962](#)).

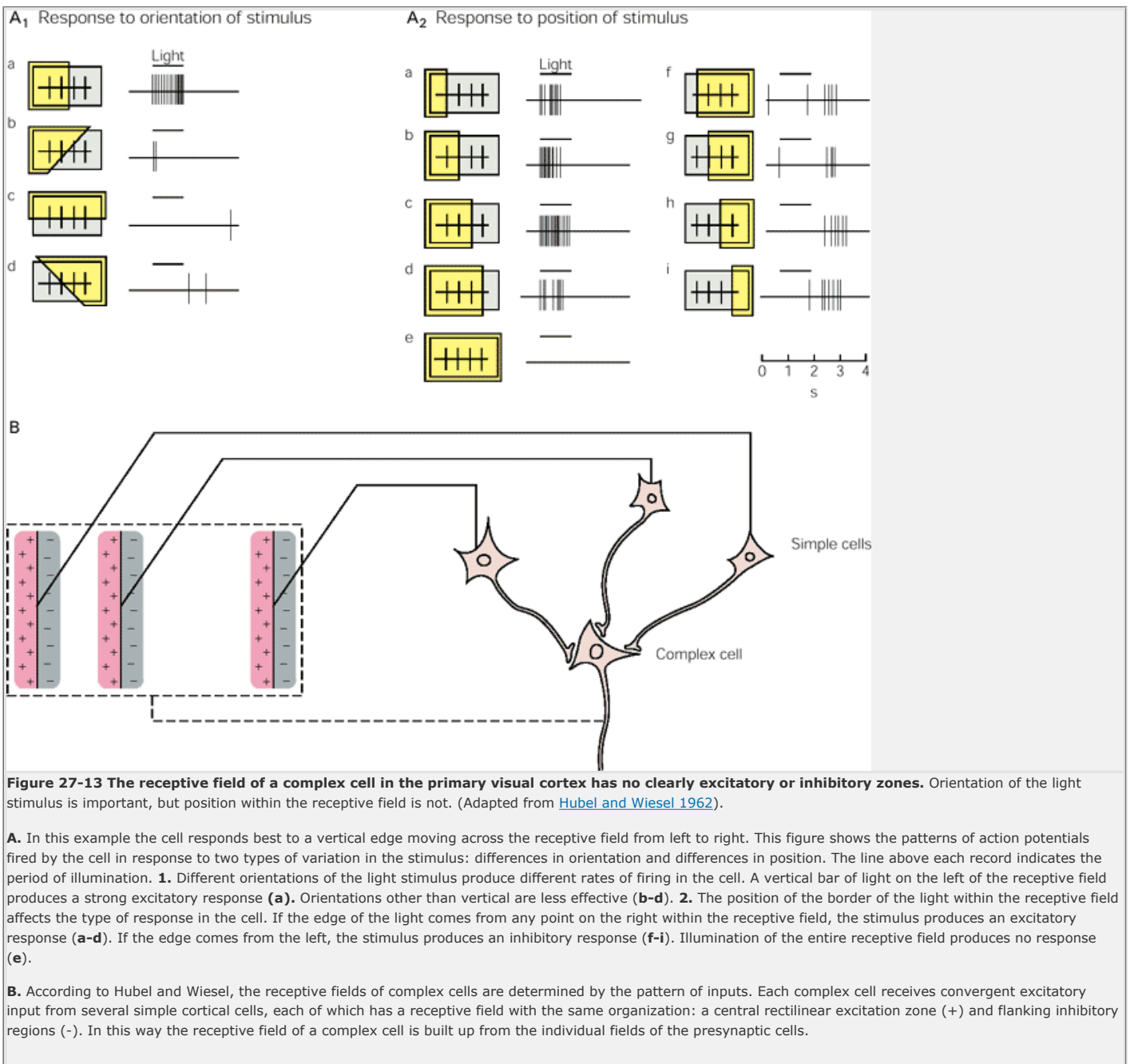
The receptive fields of *complex cells* in the cortex are usually larger than those of simple cells. These fields also have a critical axis of orientation, but the precise position of the stimulus within the receptive field is less crucial because there are no clearly defined on or off zones ([Figure 27-13A](#)). Thus, movement across the receptive field is a particularly effective stimulus for certain complex cells. Although some complex cells have direct connections with cells of layer 4C, Hubel and Wiesel proposed that a significant input to complex cells comes from a group of simple cortical cells with the same axis of orientation but with slightly offset receptive field positions ([Figure 27-13B](#)).

Some Feature Abstraction Is Accomplished by Progressive Convergence

The pattern of convergence of inputs throughout the pathway that leads to the complex cells suggests that

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each complex cell surveys the activity of a group of simple cells, each simple cell surveys the activity of a group of geniculate cells, and each geniculate cell surveys the activity of a group of retinal ganglion cells. The ganglion cells survey the activity of bipolar cells that, in turn, survey an array of receptors. At each level each cell has a greater capacity for abstraction than cells at lower levels.



At each level of the afferent pathway the stimulus properties that activate a cell become more specific. Retinal ganglion and geniculate neurons respond primarily to contrast. This elementary information is transformed

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in the simple and complex cells of the cortex, through the pattern of excitation in their rectilinear fields, into relatively precise line segments and boundaries. Hubel and Wiesel suggest that this processing is an important step in analyzing the contours of objects.

In fact, contour information may be sufficient to recognize an object. Monotonous interior or background surfaces contain no critical visual information! David Hubel describes this unexpected feature of perception:

Many people, including myself, still have trouble accepting the idea that the interior of a form... does not itself excite cells in our brain,... that our awareness of the interior as black or white.... depends only on cells' sensitivity to the borders. The intellectual argument is that perception of an evenly lit interior depends on the activation of cells having fields at the borders and on the absence of activation of cells whose fields are within the borders, since such activation would indicate that the interior is not evenly lit. So our perception of the interior as black, white, gray or green has nothing to do with cells whose fields are in the interior—hard as that may be to swallow.... What happens at the borders is the only information you need to know: the interior is boring.

It is the information carried by edges that allows us to recognize objects in a picture readily even when the objects are sketched only in rough outline (see [Figure 25-3](#)).

Since simple and complex cells in V1 receive input from both the M and P pathways, both pathways could contribute to what the theoretical biologist David Marr called the *primal sketch*, the initial two-dimensional approximation of the shape of a stimulus. We will return in [Chapter 28](#) to the fate of the P and M pathways.

The Primary Visual Cortex Is Organized Into Functional Modules

We have seen how the organization of the receptive fields of neurons in the visual pathway changes from concentric to simple to complex. Do these local transformations reflect a larger organization within the visual cortex? We shall see that the neurons in the visual cortex have a columnar organization, like the somatic sensory cortex, and that sets of columns can be regarded as functional modules, each of which processes visual information from a specific region of the visual field.

Neurons With Similar Receptive Fields Are Organized in Columns

Like the somatic sensory cortex, the primary visual cortex is organized into narrow columns of cells, running from the pial surface to the white matter. Each column is about 30 to 100 μm wide and 2 mm deep, and each contains cells in layer 4C with concentric receptive fields. Above and below are simple cells whose receptive fields

monitor almost identical retinal positions and have identical axes of orientation. For this reason these groupings are called *orientation columns*. Each orientation column also contains complex cells. The properties of these complex cells can most easily be explained by postulating that each complex cell receives direct connections from the simple cells in the column. Thus, columns in the visual system seem to be organized to allow local interconnection of cells, from which the cells are able to generate a new level of abstraction of visual information. For instance, the columns allow cortical cells to generate linear receptive field properties from the inputs of several cells in the lateral geniculate nucleus that respond best to small spots of light.

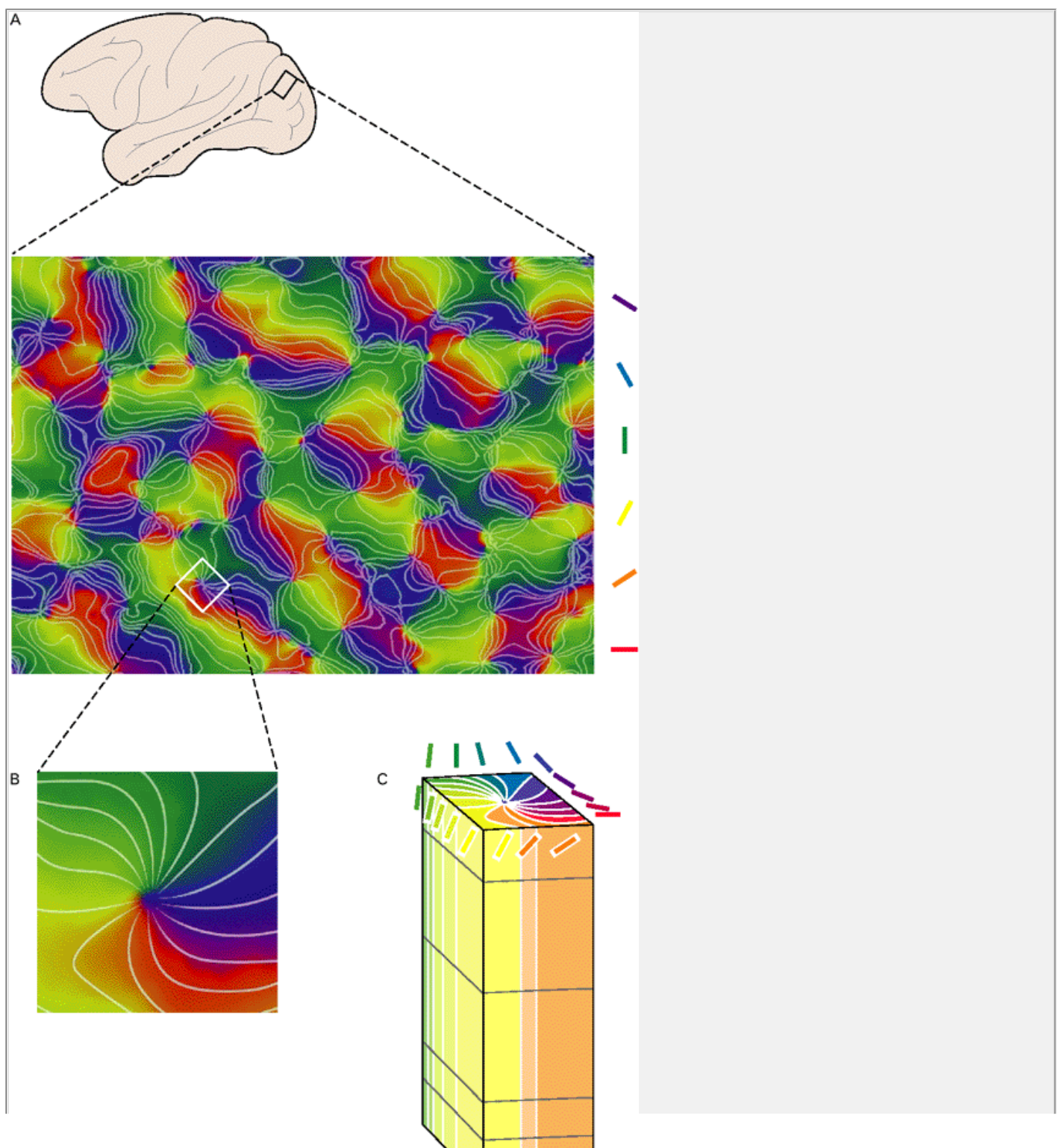
The discovery of columns in the various sensory systems was one of the most important advances in cortical physiology in the past several decades and immediately raised questions that have led to a family of new discoveries. For example, given that cells with the same axis of orientation tend to be grouped into columns, how are columns of cells with *different* axes of orientation organized in relation to one another? Detailed mapping of adjacent columns by Hubel and Wiesel, using tangential penetrations with microelectrodes, revealed a precise organization with an orderly shift in axis of orientation from one column to the next. About every three-quarters of a millimeter contained a complete cycle of orientation changes.

The anatomical layout of the orientation columns was first demonstrated in electrophysiological experiments in which marks were made in the cortex near the cells that are activated by stimuli at a given orientation. Later, this anatomical arrangement was delineated by injecting 2-deoxyglucose, a glucose analog that can be radiolabeled and injected into the brain. Cells that are metabolically active take up the label and can then be detected when sections of cortex are overlaid with x-ray film. Thus, when a stimulus of lines with a given orientation is presented, an orderly array of active and inactive stripes of cells is revealed. A remarkable advance now allows the different orientation columns to be visualized directly in the living cortex. Using either a voltage-sensitive dye or inherent differences in the light scattering of active and inactive cells, a highly sensitive camera can detect the pattern of active and inactive orientation columns during presentation of a bar of light with a specific axis of orientation ([Figure 27-14](#)).

The systematic shifts in axis of orientation from one column to another is occasionally interrupted by *blobs*, the peg-shaped regions of cells prominent in layers P.538

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2 and 3 of V1 ([Figure 27-15](#)). The cells in the blobs frequently respond to different color stimuli, and their receptive fields, like those of cells in the lateral geniculate nucleus, have no specific orientation.



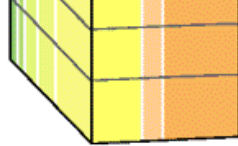


Figure 27-14 Orientation columns in the visual cortex of the monkey. (Courtesy of Gary Blasdel.)

A. Image of a 9 by 12 mm rectangle of cortical surface taken while the monkey viewed contours of different orientations (indicated on the right). This image was obtained through optical imaging and by comparing local changes in reflectance, which indicate activity. Areas that were most active during the presentation of a particular orientation are indicated by the color chosen to represent that orientation (bars on the right). Complementary colors were chosen to represent orthogonal orientations. Hence, red and green indicate maximal activities in response to horizontal and vertical, while blue and yellow indicate greatest activation by left and right oblique.

B. Enlargement of a pinwheel-like area in A. Orientations producing the greatest activity remain constant along radials, extending outward from a center, but change continuously (through $\pm 18^\circ$).

C. Three-dimensional organization of orientation columns in a 1 mm \times 1 mm \times 2 mm slab of primary visual cortex underlying the square surface region depicted in B.

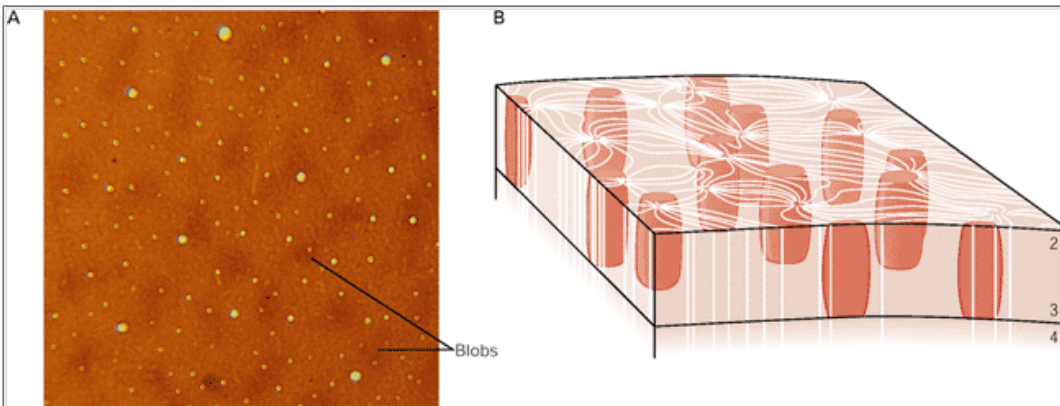


Figure 27-15 Organization of blobs in the visual cortex.

A. Blobs are visible as dark patches in this photograph of a single 40µm thick layer of upper cortex that has been processed histochemically to reveal the density of cytochrome oxidase, a mitochondrial enzyme involved in energy production. The heightened enzymatic activity in the blobs is thought to represent heightened neural activity. The cortex was sectioned tangentially. (Courtesy of D. Ts'o, C. Gilbert, and T. Wiesel.)

B. Organization of the blobs in relation to the orientation columns. Only the upper layers of the cortex are shown with the blobs extending through these layers. The blobs interrupt the pattern of the orientation columns.

In addition to columns of cells responsive to axis of orientation and blobs related to color processing, a third system of alternating columns processes separate inputs from each eye. These *ocular dominance* columns, which we shall consider again in [Chapter 56](#), represent an orderly arrangement of cells that receive inputs only from the left or right eye and are important for binocular interaction. The ocular dominance columns have been visualized using transsynaptic transport of radiolabeled amino acids injected into one eye. In autoradiographs of sections of cortex cut perpendicular to the layers, patches in layer 4 that receive input from the injected eye are heavily labeled, and they alternate with unlabeled patches that mediate input from the uninjected eye ([Figure 27-16](#)).

A Hypercolumn Represents the Visual Properties of One Region of the Visual Field

Hubel and Wiesel introduced the term *hypercolumn* to refer to a set of columns responsive to lines of all orientations from a particular region in space. The relationship between the orientation columns, the independent ocular dominance columns, and the blobs within a module is illustrated in [Figure 27-17](#). A complete sequence of ocular dominance columns and orientation columns is repeated regularly and precisely over the surface of the primary visual cortex, each occupying a region of about 1 mm². This repeating organization is a striking illustration of the modular organization characteristic of the cerebral cortex. Each module acts as a window on the visual field and each window represents only a tiny part of the visual field, but the whole field is covered by many such windows. Within the processing module all information about that part of the visual world is processed. From what we know now, that includes orientation, binocular interaction, color, and motion.

Each module has a variety of outputs originating in different cortical layers. The organization of the output connections from the primary visual cortex is similar to that of the somatic sensory cortex in that there are outputs from all layers except 4C, and in each layer the principal output cells are the pyramidal cells (see [Figure 27-10C](#)). The axons of cells above layer 4C project to other cortical areas; those of cells below 4C project to subcortical areas. The cells in layers 2 and 3 send their output to other higher visual cortical regions, such as Brodmann's area 18 (V2, V3, and V4). They also make connections via the corpus callosum to anatomically symmetrical cortical areas on the other side of the brain. Cells in layer 4B project to the middle temporal area (V5 or MT). Cells in layer 5 project to the superior colliculus, the pons, and the pulvinar. Cells in layer 6 project back to the lateral geniculate nucleus and to the claustrum.

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Since cells in each layer of the visual cortex probably perform a different task, the laminar position of a cell determines its functional properties.

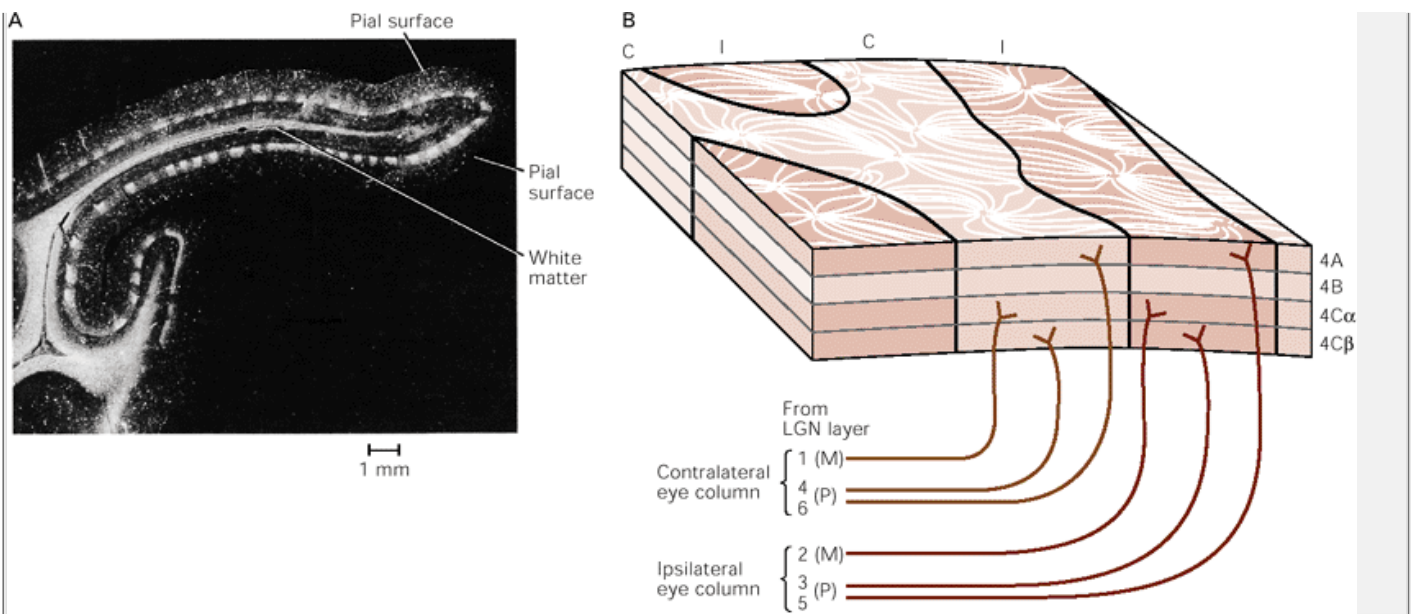


Figure 27-16 The ocular dominance columns.

A. This autoradiograph of the primary visual cortex of an adult monkey shows the ocular dominance columns as alternating white and dark (labeled and unlabeled) patches in layer 4 of the cortex, below the pial surface. One eye of the monkey was injected with a cell label, which over the course of 2 weeks was transported to the lateral geniculate nucleus and then across synapses to the geniculocortical relay cells, whose axons terminate in layer 4 of the visual cortex. Areas of layer 4 that receive input from the injected eye are heavily labeled and appear white; the alternating unlabeled patches receive input from the uninjected eye. In all, some 56 columns can be counted in layer 4C. The underlying white matter appears white because it contains the labeled axons of geniculate cells. (From [Hubel and Wiesel, 1979](#).)

B. The scheme of inputs to the alternating ocular dominance columns in layer 4 of the primary visual cortex. Inputs from the contralateral (C) and ipsilateral (I) eyes arise in different layers in the lateral geniculate nucleus (LGN), identified in [Figure 27-5](#), and project to different subdivisions of layer 4.

Columnar Units Are Linked by Horizontal Connections

As we have seen, three major vertically oriented systems crossing the layers of primary visual cortex have been delineated: (1) orientation columns, which contain the neurons that respond selectively to light bars with specific axes of orientation; (2) blobs, peg-shaped patches in upper layers (but not layer 4) that contain cells that are more concerned with color than orientation; and (3) ocular dominance columns, which receive inputs from one or the other eye. These units are organized into hypercolumns that monitor small areas of the visual field.

These vertically oriented systems communicate with one another by means of horizontal connections that link cells within a layer. Axon collaterals of individual pyramidal cells in layers 3 and 5 run long distances, parallel with the layers, and give rise to clusters of axon terminals at regular intervals that approximate the width of a hypercolumn ([Figure 27-18A](#)). Horseradish peroxidase injected into focal regions within superficial cortical layers (2, 3) reveals an elaborate lattice of labeled cells and axons that encloses unlabeled patches about 500 μm in diameter. Similarly, tracers injected into sites corresponding to blobs label other blobs, producing a honeycomb image. A honeycomb array also appears after labeling the nonblob cortex.

To examine these horizontal connections, recordings were made from pairs of cells in blob regions; each pair was separated by about 1 mm, the distance that typically separates the lattice arrays described above ([Figure 27-18B](#)). Many cell pairs were found to fire simultaneously in response to stimuli with a specific orientation and direction of movement. Thus, color-selective cells in one blob are linked to cells with similar responses in other blobs.

Additional evidence that horizontal connections tie together cells with similar response properties in different columns comes from injection of radiolabeled 2-deoxyglucose and fluorescently labeled microbeads

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into a column containing cells that respond to a specific orientation. The beads are taken up by axon terminals at the injection site and transported back to the cell bodies. In sections tangential to the pia the overall pattern of cells labeled with the microbeads closely resembles the lattice described above. In fact, the pattern labeled with 2-deoxyglucose is congruent with the pattern obtained with the microbeads ([Figure 27-18C](#)). Thus, both anatomical and metabolic studies establish that cortical cells having receptive fields with the same orientation are connected by means of a horizontal network.

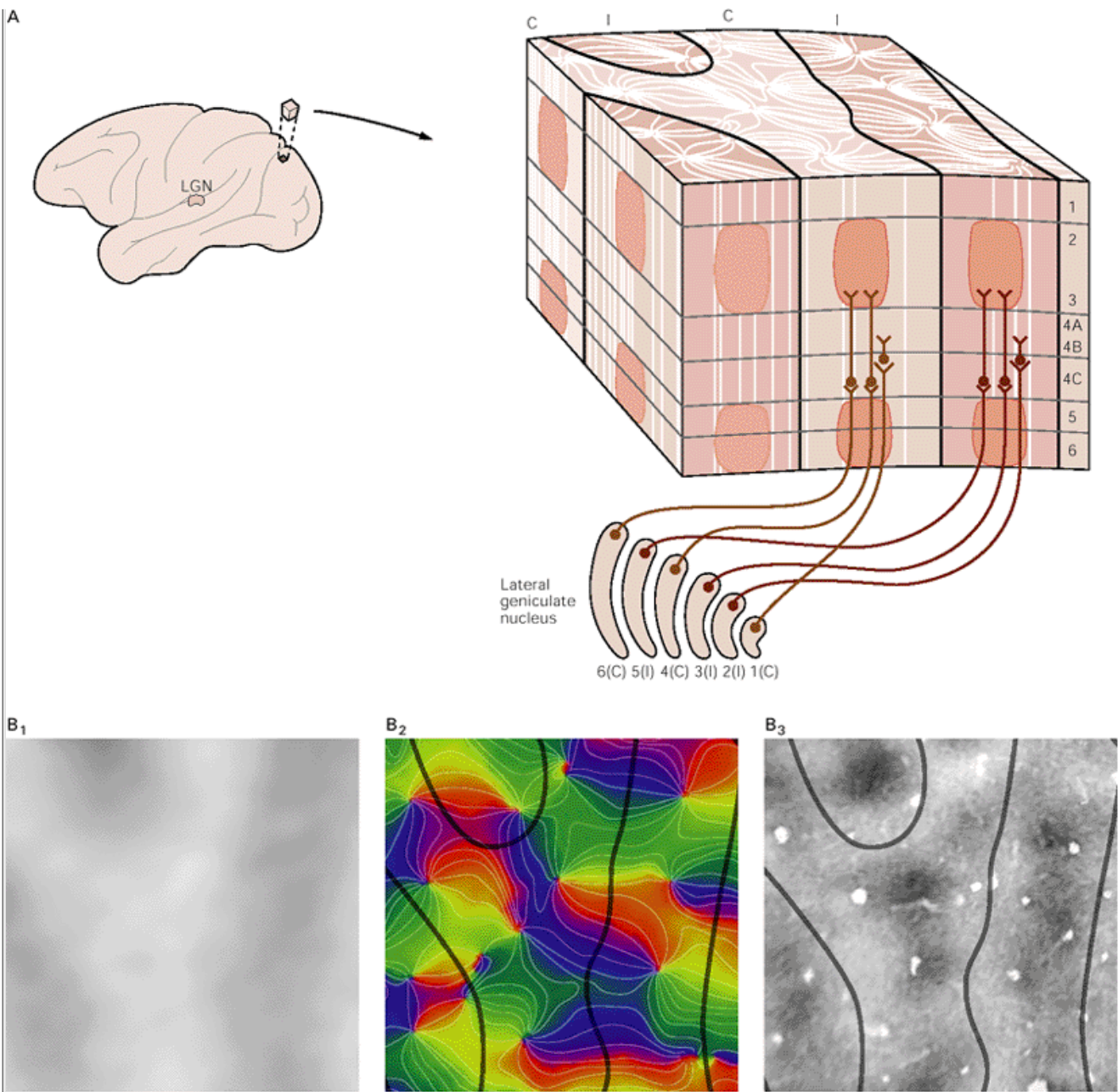


Figure 27-17 Organization of orientation columns, ocular dominance columns, and blobs in primary visual cortex.

A. An array of functional columns of cells in the visual cortex contains the neural machinery necessary to analyze a discrete region of the visual field and can be thought of as a functional *module*. Each module contains one complete set of orientation columns, one set of ocular dominance columns (right and left eye), and several blobs (regions of the cortex associated with color processing). The entire visual field can be represented in the visual cortex by a regular array of such modules.

B. Images depicting ocular dominance columns, orientation columns, and blobs from the same region of primary visual cortex. (Courtesy of Gary Blasdel.) **1.** Images of ocular dominance columns were obtained using optical imaging and independently stimulating the left and right ocular dominance columns in a particular region. Because neural activity decreases cortical reflectance, the subtraction of one left eye image from one right eye image produces the characteristic pattern of dark and light bands, representing the right and left eyes respectively. **2.** In this image the borders of the ocular dominance columns shown in 1 appear as **black lines** superimposed on the pattern of orientation-specific columns depicted in [Figure 27-14](#). **3.** The borders of the ocular dominance columns shown in 1 are superimposed on tissue reacted for cytochrome oxidase, which visualizes the blobs. The blobs are thus seen localized in the centers of the ocular dominance columns.

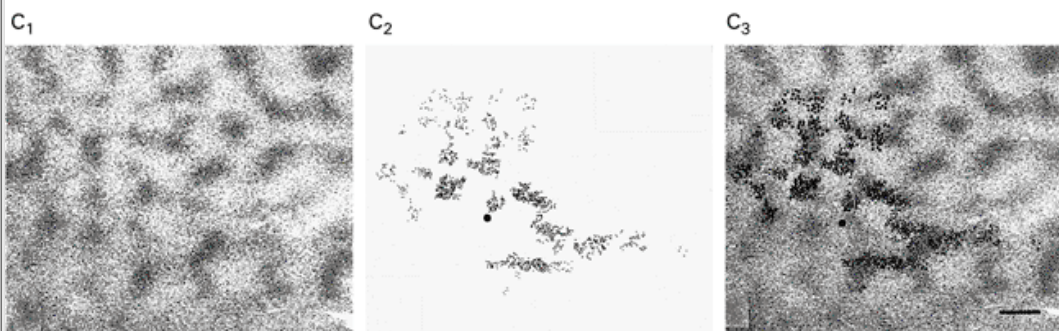
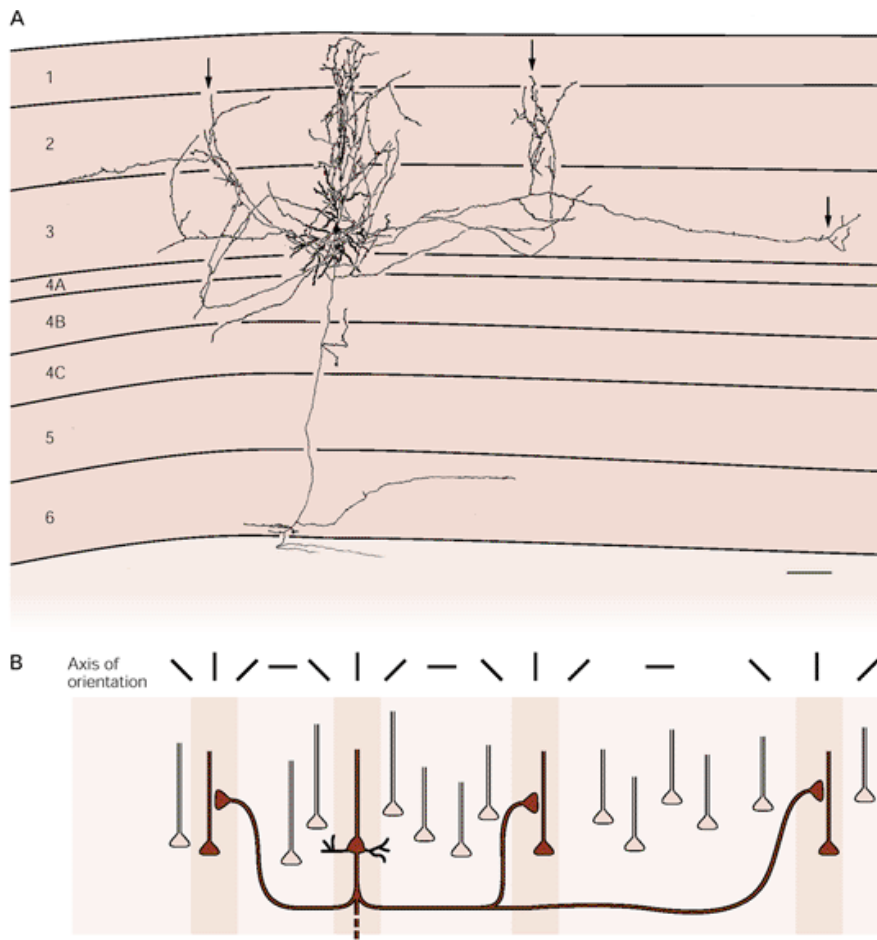


Figure 27-18 Columns of cells in the visual cortex with similar function are linked through horizontal connections.

A. A camera lucida reconstruction of a pyramidal cell injected with horseradish peroxidase in layers 2 and 3 in a monkey. Several axon collaterals branch off the descending axon near the dendritic tree and in three other clusters (**arrows**). The clustered collaterals project vertically into several layers at regular intervals, consistent with the sequence of functional columns of cells. (From [McGuire et al. 1991](#).)

B. The horizontal connections of a pyramidal cell, such as that shown in A, are functionally specific. The axon of the pyramidal cell forms synapses on other pyramidal cells in the immediate vicinity as well as pyramidal cells some distance away. Recordings of cell activity demonstrate that the axon makes connections only with cells that have the same functional specificity (in this case, responsiveness to a vertical line). (Adapted from [Ts'o et al. 1986](#).)

C. 1. A section of cortex labeled with 2-deoxyglucose shows a pattern of stripes representing columns of cells that respond to a stimulus with a particular orientation. **2.** Microbeads injected into the same site as in 1 are taken up by the terminals of neurons and transported to the cell bodies. **3.** Superimposition of the images in 1 and 2. The clusters of bead-labeled cells lie directly over the 2-deoxyglucose-labeled areas, showing that groups of cells in different columns with the same axis of orientation are connected. (From [Gilbert and Wiesel 1989](#).)

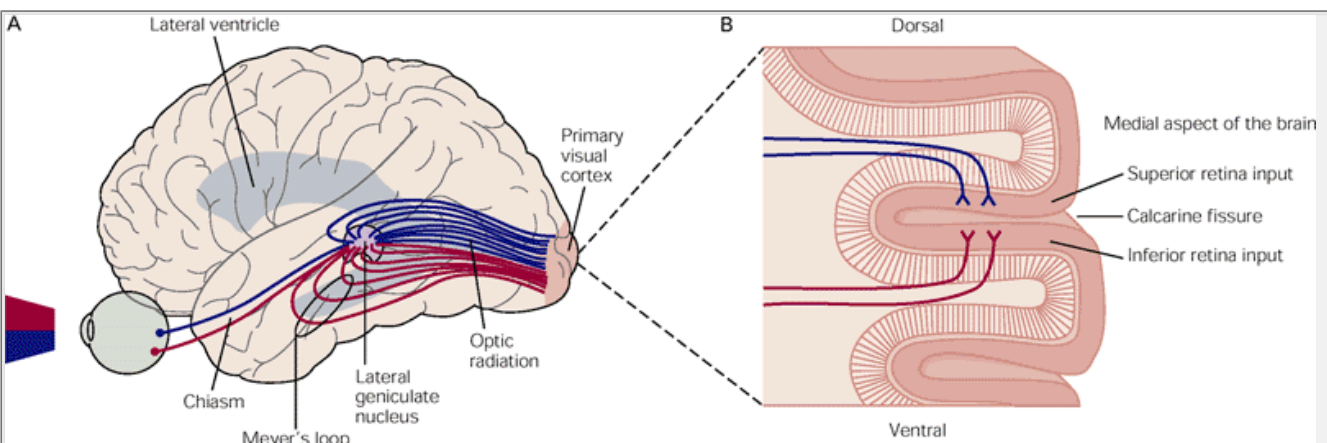


Figure 27-19 Projection of input from the retina to the visual cortex.

A. Fibers from the lateral geniculate nucleus sweep around the lateral ventricle in the *optic radiation* to reach the primary visual cortex. Fibers that relay inputs from the inferior half of the retina loop rostrally around the temporal horn of the lateral ventricle, forming Meyer's loop. (Adapted from Brodal 1981.)

B. A cross section through the primary visual cortex in the occipital lobe. Fibers that relay input from the inferior half of the retina terminate in the inferior bank of the visual cortex, below the calcarine fissure. Those that relay input from the superior half of the retina terminate in the superior bank.

The visual cortex, then, is organized functionally into two sets of intersecting connections, one vertical, consisting of functional columns spanning the different cortical layers, and the other horizontal, connecting functional columns with the same response properties. What is the functional importance of the horizontal connections? Recent studies indicate that these connections integrate information over many millimeters of cortex. As a result, a cell can be influenced by stimuli *outside* its normal receptive field. Indeed, a cell's axis of orientation is not completely invariant but is dependent on the context on which the feature is embedded. The psycho-physical principle of *contextual effect*, whereby we evaluate objects in the context in which we see them, is thought to be mediated by the horizontal connections between the functional columns of the visual cortex.

Lesions in the Retino-Geniculate-Cortical Pathway Are Associated With Specific Gaps in the Visual Field

As we have seen in [Chapter 20](#), the fact that the connections between neurons in the brain are precise and relate to behavior in an orderly way allows one to infer the site of anatomical lesions from a clinical examination of a patient. Lesions along the visual pathway produce characteristic gaps in the visual field.

The axons in the optic tract form synapses on the principal cells of the lateral geniculate nucleus. In turn, the axons of the principal cells sweep around the lateral ventricle in the optic radiation to the primary visual cortex, radiating on the lateral surface of both the temporal and occipital horns of the lateral ventricle ([Figure 27-19A](#)). Fibers representing the inferior parts of the retina swing rostrally in a broad arc over the temporal horn of the ventricle and loop into the temporal lobe before turning caudally to reach the occipital pole. This group of fibers, called *Meyer's loop*, relays input from the inferior half of the retina terminate in the inferior bank of the cortex lining the calcarine fissure. The fibers relaying input from the superior half of the retina terminate in the superior bank ([Figure 27-19B](#)). Consequently, unilateral lesions in the temporal lobe affect vision in the superior quadrant of the contralateral visual hemifield

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because they disrupt Meyer's loop. A lesion in the inferior bank of the calcarine cortex causes a gap in the superior half of the contralateral visual field.

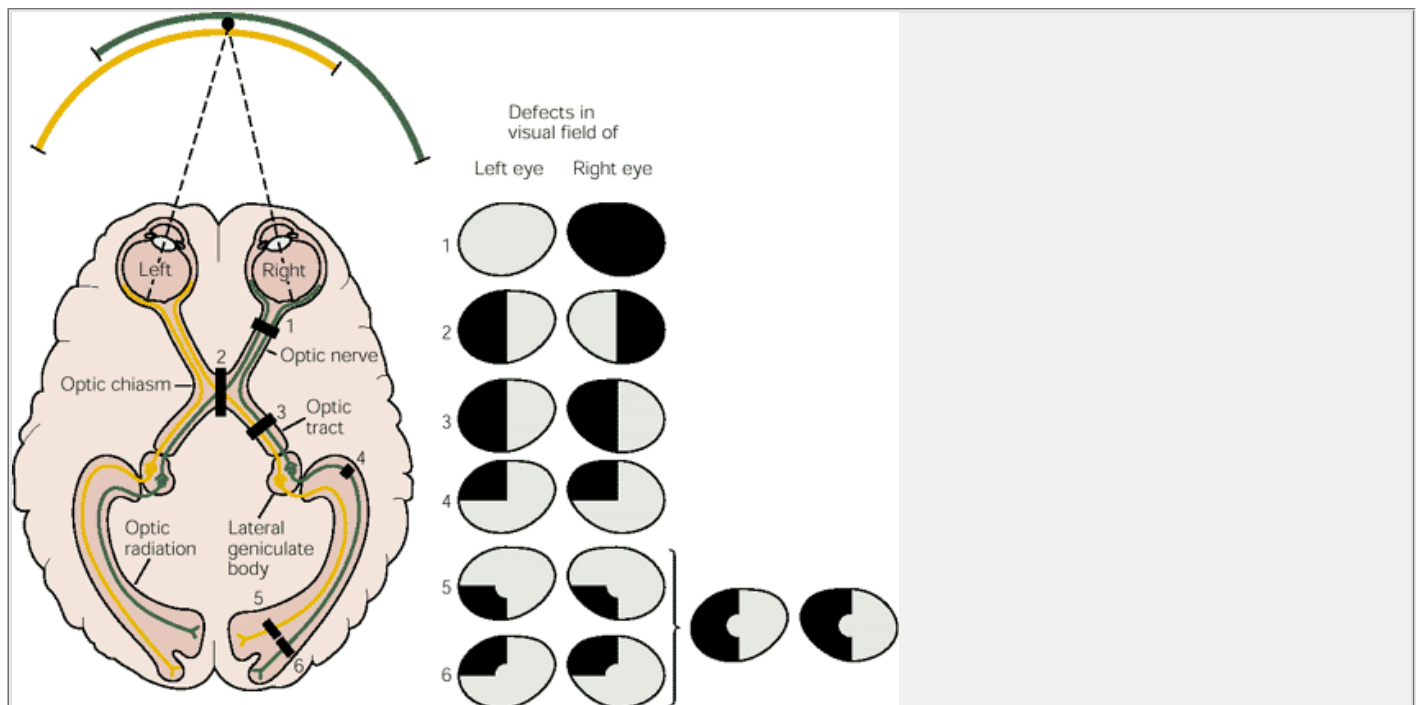


Figure 27-20 Deficits in the visual field produced by lesions at various points in the visual pathway. The level of a lesion can be determined by the specific deficit in the visual field. In the diagram of the cortex the numbers along the visual pathway indicate the sites of lesions. The deficits that result from lesions at each site are shown in the visual field maps on the right as **black areas**. Deficits in the visual field of the left eye represent what an individual would *not* see with the right eye closed rather than deficits of the left visual hemifield.

1. A lesion of the right optic nerve causes a total loss of vision in the right eye.

2. A lesion of the optic chiasm causes a loss of vision in the temporal halves of both visual fields (bitemporal hemianopsia). Because the chiasm carries crossing fibers from both eyes, this is the only lesion in the visual system that causes a *nonhomonymous* deficit in vision, ie, a deficit in two different parts of the visual field resulting from a single lesion.

3. A lesion of the optic tract causes a complete loss of vision in the opposite half of the visual field (contralateral hemianopsia). In this case, because the lesion is on the right side, vision loss occurs on the left side.

4. After leaving the lateral geniculate nucleus the fibers representing both retinas mix in the optic radiation (see [Figure 27-19](#)). A lesion of the optic radiation fibers that curve into the temporal lobe (Meyer's loop) causes a loss of vision in the upper quadrant of the opposite half of the visual field of both eyes (upper contralateral quadrantic anopsia).

5, 6. Partial lesions of the visual cortex lead to partial field deficits on the opposite side. A lesion in the upper bank of the calcarine sulcus (**5**) causes a partial deficit in the inferior quadrant of the visual field on the opposite side. A lesion in the lower bank of the calcarine sulcus (**6**) causes a partial deficit in the superior quadrant of the visual field on the opposite side. A more extensive lesion of the visual cortex, including parts of both banks of the calcarine cortex, would cause a more extensive loss of vision in the contralateral hemifield. The central area of the visual field is unaffected by cortical lesions (**5** and **6**), probably because the representation of the foveal region of the retina is so extensive that a single lesion is unlikely to destroy the entire representation. The representation of the periphery of the visual field is smaller and hence more easily destroyed by a single lesion.

This arrangement illustrates a key principle: At the initial stages of visual processing each half of the brain is concerned with the contralateral hemifield of vision. This pattern of organization begins with the segregation of axons in the optic chiasm, where fibers from the two eyes dealing with the same part of the visual field are brought together (see [Figure 27-1](#)). In essence, this is similar to the somatic sensory system, in which each hemisphere mediates sensation on the contralateral side of the body.

We can understand better the projection of the visual world onto the primary visual cortex by considering the gaps in the visual field produced by lesions at various levels leading up to the cortex. These deficits are summarized in [Figure 27-20](#).

After sectioning one optic nerve the visual field is seen monocularly by the eye on the intact side ([Figure 27-20, 1](#)).

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The temporal crescent is normally seen only by the nasal hemiretina on the same side. A person whose optic nerve is cut would therefore be blind in the temporal crescent on the lesioned side. Removal of binocular input in this way also affects the perception of spatial depth (stereopsis).

Destruction of the fibers crossing in the optic chiasm removes input from the temporal portions of both halves of the visual field. The deficit produced by this lesion is called *bitemporal hemianopsia* and occurs because fibers arising from the nasal half of each retina have been destroyed ([Figure 27-20, 2](#)). This kind of damage is most commonly caused by a tumor of the pituitary gland that compresses the chiasm.

Destruction of one optic tract produces *homonymous hemianopsia*, a loss of vision in the entire contralateral visual hemifield ([Figure 27-20, 3](#)). For example, destruction of the right tract causes left homonymous hemianopsia, ie, loss of vision in the left nasal and right temporal hemiretinas ([Figure 27-20, 4](#)). Finally, a lesion of the optic radiation or of the visual cortex, where the fibers are more spread out, produces an *incomplete or quadrant field defect*, a loss of vision in part of the contralateral visual hemifield ([Figure 27-20, 5, 6](#)).

An Overall View

Visual information important for perception flows from the retina to the lateral geniculate nucleus. In both structures cells have small circular receptive fields. The primary visual cortex elaborates the elemental information from these cells in at least three ways. (1) Each part of the visual field is decomposed into short line segments of different orientation, through orientation columns. This is an early step in the process thought to be necessary for discrimination of form. (2) Color processing occurs in cells that lack orientation selectivity in regions called blobs. (3) The input from the two eyes is combined through the ocular dominance columns, a step necessary for perception of depth.

This parallel processing in the visual system is achieved by means of central connections that are remarkably specific. The ganglion cells in the retina project to the lateral geniculate nucleus in the thalamus in an orderly way that creates a complete retinotopic map of the visual field for each eye in the nucleus. Furthermore, the M and P ganglion cells of the retina project to different layers of the lateral geniculate nucleus: the M cells to the magnocellular layers and the P cells to the parvocellular layers. Cells in these layers project to different sublayers in 4C of striate cortex (4C α and 4C β). Thus, two separate pathways (the M and P pathways) extend from the retina to the primary visual cortex. The functional contribution of the M and P pathways are different. The P pathway is essential for color vision and is particularly sensitive to stimuli with higher spatial and lower temporal frequencies. The M pathway is more sensitive to stimuli with lower spatial and higher temporal frequencies.

Within the striate cortex each geniculate axon terminates primarily in layer 4, from which information is distributed to other layers, each of which has its own pattern of connections with other cortical or subcortical regions. In addition to the circuitry of the layers, cells in the visual cortex are arranged into vertically oriented functional systems: orientation-specific columns, ocular dominance columns, and blobs. Neurons with similar response properties in different vertically oriented systems are linked by horizontal connections. Information thus flows in two directions: between layers and horizontally throughout each layer. This pattern of interconnection links several columnar systems together; for example, a set of linked orientation-specific columns would represent all directions of movement in a specific region of the visual field. Such "hypercolumns" seem to function as elementary computational modules—they receive varied inputs, transform them, and send their output to a number of different regions of the brain.

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Perception of Motion, Depth, and Form

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Eric R. Kandel

IN VISION, AS IN OTHER mental operations, we experience the world as a whole. Independent attributes—motion, depth, form, and color—are coordinated into a single visual image. In the two previous chapters we began to consider how two parallel pathways—the magnocellular and parvocellular pathways, that extend from the retina through the lateral geniculate nucleus of the thalamus to the primary visual (striate) cortex—might produce a coherent visual image. In this chapter we examine how the information from these two pathways feeds into multiple higher-order centers of visual processing in the extrastriate cortex. How do these pathways contribute to our perception of motion, depth, form, and color?

The magnocellular (M) and parvocellular (P) pathways feed into two extrastriate cortical pathways: a dorsal pathway and a ventral pathway. In this chapter we examine, in cell-biological terms, the information processing in each of these pathways.

We shall first consider the perception of motion and depth, mediated in large part by the dorsal pathway to the posterior parietal cortex. We then consider the perception of contrast and contours, mediated largely by the ventral pathway extending to the inferior temporal cortex. This pathway also is concerned with the assessment of color, which we will consider in [Chapter 29](#). Finally, we shall consider the binding problem in the visual system: how information conveyed in parallel but separate pathways is brought together into a coherent perception.

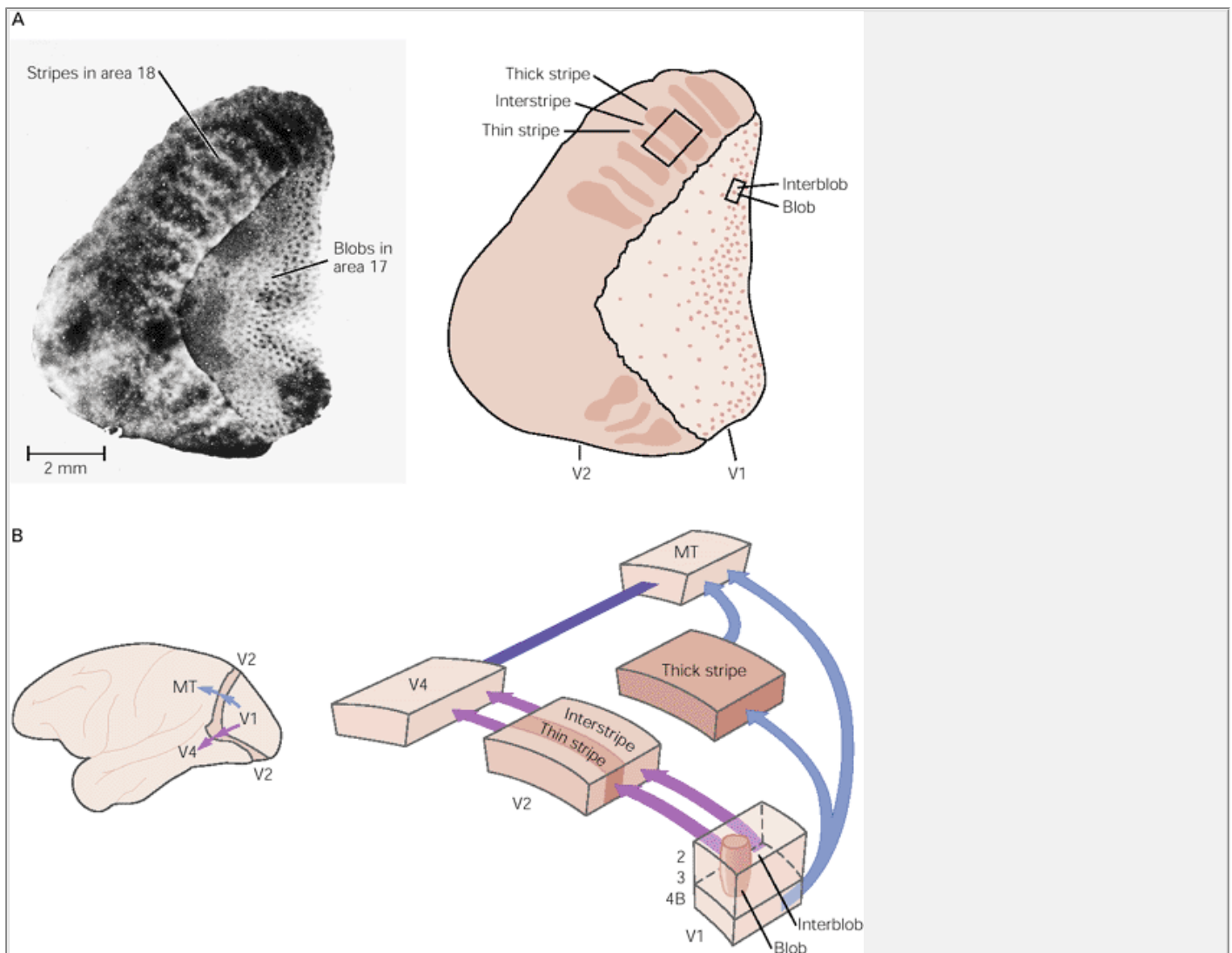


Figure 28-1 Organization of V1 and V2.

A. Subregions in V1 (area 17) and V2 (area 18). This section from the occipital lobe of a squirrel monkey at the border of areas 17 and 18 was reacted with cytochrome oxidase. The cytochrome oxidase stains the blobs in V1 and the thick and thin stripes in V2. (Courtesy of M. Livingstone.)

B. Connections between V1 and V2. The blobs in V1 connect primarily to the thin stripes in V2, while the interblobs in V1 connect to interstripes in V2. Layer 4B projects to the thick stripes in V2 and to the middle temporal area (MT). Both thin and interstripes project to V4. Thick stripes in V2 also project to MT.

The Parvocellular and Magnocellular Pathways Feed Into Two Processing Pathways in Extrastriate Cortex

In [Chapter 27](#) we saw that the parallel parvocellular and magnocellular pathways remain segregated even in the striate cortex. What happens to these P and M pathways beyond the striate cortex? Early research on these pathways indicated that the P pathway continues in the ventral cortical pathway that extends to the

inferior temporal cortex, and that the M pathway becomes the dorsal pathway that extends to the posterior parietal cortex. However, the actual relationships are probably not so exclusive.

The evidence for separation of function of the dorsal and ventral pathways begins in the primary visual, or striate, cortex (V1). Staining for the mitochondrial enzyme cytochrome oxidase reveals a precise and repeating pattern of dark, peg-like regions about 0.2 mm in diameter called blobs. The blobs are especially prominent in the superficial layers 2 and 3, where they are separated by intervening regions that stain lighter, the interblob

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regions. The same stain also reveals alternating thick and thin stripes separated by interstripes of little activity (Figure 28-1 in the secondary visual cortex, or V2).

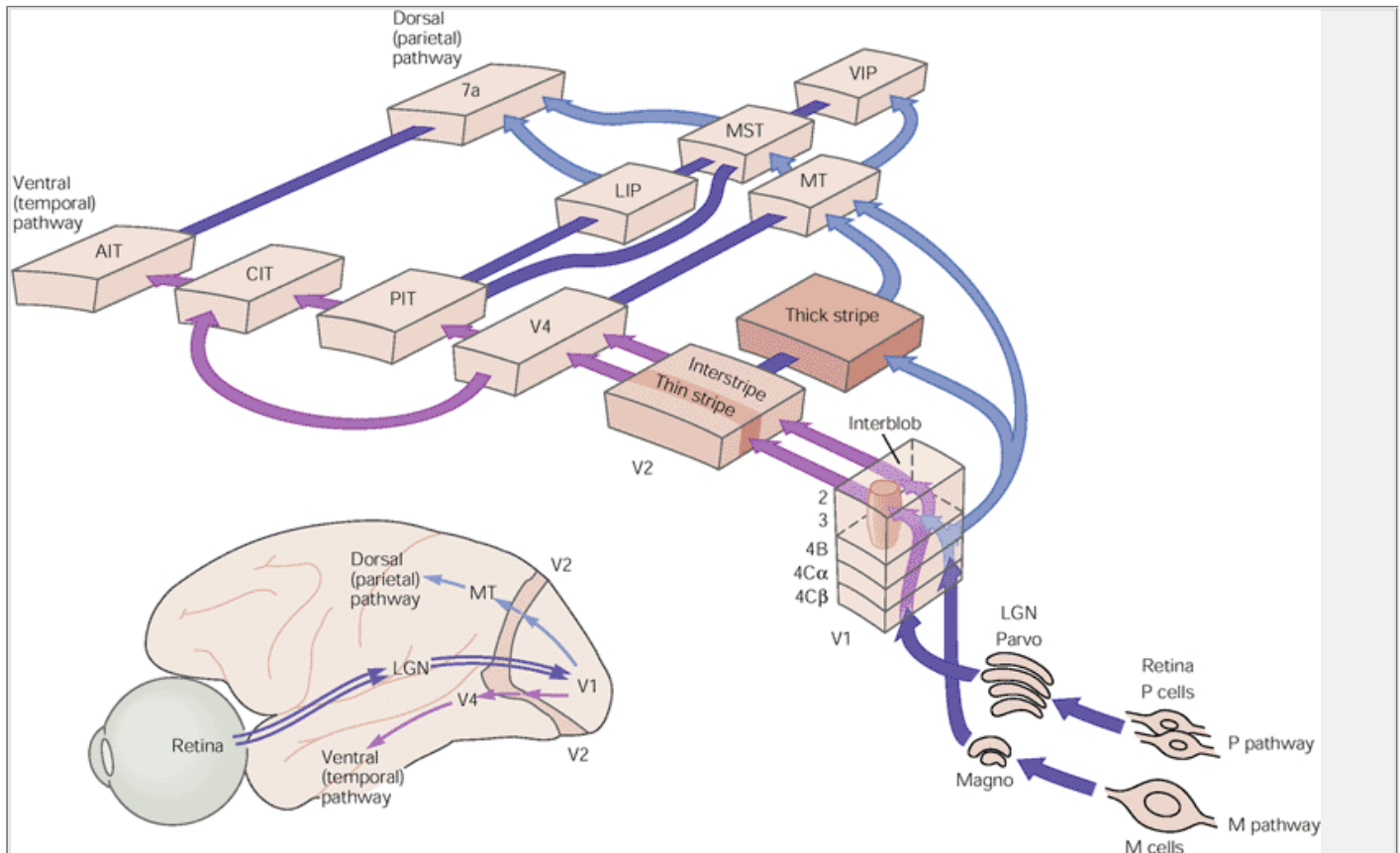


Figure 28-2 The magnocellular (M) and parvocellular (P) pathways from the retina project through the lateral geniculate nucleus (LGN) to V1.

Separate pathways to the temporal and parietal cortices course through the extrastriate cortex beginning in V2. The connections shown in the figure are based on established anatomical connections, but only selected connections are shown and many cortical areas are omitted (compare Figure 25-9). Note the cross connections between the two pathways in several cortical areas. The parietal pathway receives input from the M pathway but only the temporal pathway receives input from both the M and P pathways. (Abbreviations: **AIT** = anterior inferior temporal area; **CIT** = central inferior temporal area; **LIP** = lateral intraparietal area; **Magno** = magnocellular layers of the lateral geniculate nucleus; **MST** = medial superior temporal area; **MT** = middle temporal area; **Parvo** = parvocellular layers of the lateral geniculate nucleus; **PIT** = posterior inferior temporal area; **VIP** = ventral intraparietal area.) (Based on Merigan and Maunsell 1993.)

Margaret Livingstone and David Hubel identified the anatomical connections between labeled regions in V1 and V2 (Figure 28-1B). They found that the P and M pathways remain partially segregated through V2. The M pathway projects from the magnocellular layers of the lateral geniculate nucleus to the striate cortex, first to layer 4C α and then to layer 4B. Cells in layer 4B project directly to the middle temporal area (MT) and also to the thick stripes in V2, from which cells also project to MT. Thus, a clear anatomical pathway exists from the magnocellular layers in the lateral geniculate nucleus to MT and from there to the posterior parietal cortex (Figure 28-2).

Cells in the parvocellular layers of the lateral geniculate nucleus project to layer 4C β in the striate cortex, from which cells project to the blobs and interblobs of V1. The blobs send a strong projection to the thin stripes in V2, whereas interblobs send a strong projection to the interstripes in V2. The thin stripe and interstripe areas of V2 may in turn project to discrete subregions of V4, thus maintaining this separation in the P pathway into V4 and possibly on into the inferior temporal cortex. A pathway from the P cells in the lateral geniculate nucleus

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to the inferior temporal cortex can therefore also be identified (Figure 28-2).

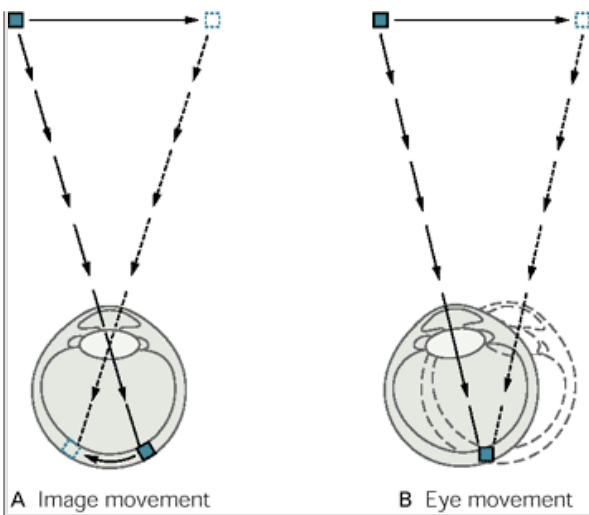


Figure 28-3 Motion in the visual field can be perceived in two ways.

A. When the eyes are held still, the image of a moving object traverses the retina. Information about movement depends upon sequential firing of receptors in the retina. **B.** When the eyes follow an object, the image of the moving object falls on one place on the retina and the information is conveyed by movement of the eyes or the head.

But are these pathways exclusive of each other? Several anatomical observations suggest that they are not. In V1 both the magnocellular and parvocellular pathways have inputs in the blobs, and local neurons make extensive connections between the blob and interblob compartments. In V2 cross connections exist between the stripe compartments. Thus, the separation is not absolute, but whether there is an intermixing of the M and P contributions or whether the cross connections allow one cortical pathway to modulate activity in the other is not clear.

Results of experiments that selectively inactivate the P and M pathways as they pass through the lateral geniculate nucleus (described in [Chapter 27](#)) also erode the notion of strict segregation between the pathways in V1. Blocking of either pathway affects the responses of fewer than half the neurons in V1, which indicates that most V1 neurons receive physiologically effective inputs from both pathways. Further work has shown that the responses of neurons both within and outside of the blobs in the superficial layers of V1 are altered by blocking only the M pathway. Both observations suggest that there is incomplete segregation of the M and P pathways in V1.

This selective blocking of the P and M pathways also reveals the relative contributions of the pathways to the parietal and inferior temporal cortices. Blocking the magnocellular layers of the lateral geniculate nucleus eliminates the responses of many cells in MT and always reduces the responses of the remaining cells; blocking the parvocellular layers produces a much weaker effect on cells in MT. In contrast, blocking the activity of either the parvocellular or magnocellular layers in the lateral geniculate nucleus reduces the activity of neurons in V4. Thus, the dorsal pathway to MT seems primarily to include input from the M pathway, whereas the ventral pathway to the inferior temporal cortex appears to include input from both the M and P pathways. We can now see that there is substantial segregation of the P and M pathways up to V1, probably

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separation into V2, a likely predominance of the M input to the dorsal pathway to MT and the parietal cortex, and a mixture of P and M input into the pathway leading to the inferior temporal lobe (as indicated by the lines crossing between the pathways in [Figure 28-2](#)).

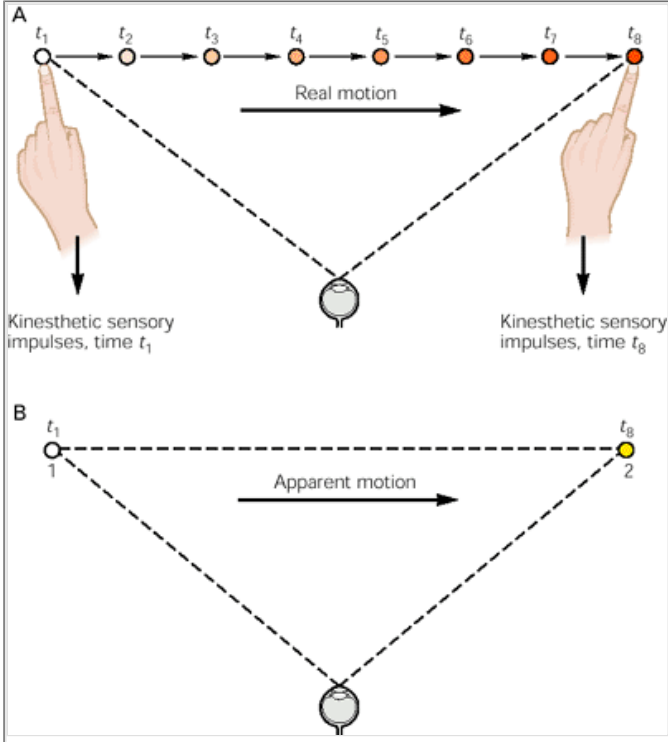


Figure 28-4 The illusion of apparent motion is evidence that the visual system analyzes motion in a separate pathway.

A. Actual motion is experienced as a sequence of visual sensations, each resulting from the image falling on a different position in the retina.

B. Apparent motion may actually be more convincing than actual motion, and is the perceptual basis for motion pictures. Thus, when two lights at positions **1** and **2** are turned on and off at suitable intervals, we perceive a single light moving between the two points. This perceptual illusion cannot be explained by processing of information based on different retinal positions and is therefore evidence for the existence of a special visual system for the detection of motion. (From Hochberg 1978.)

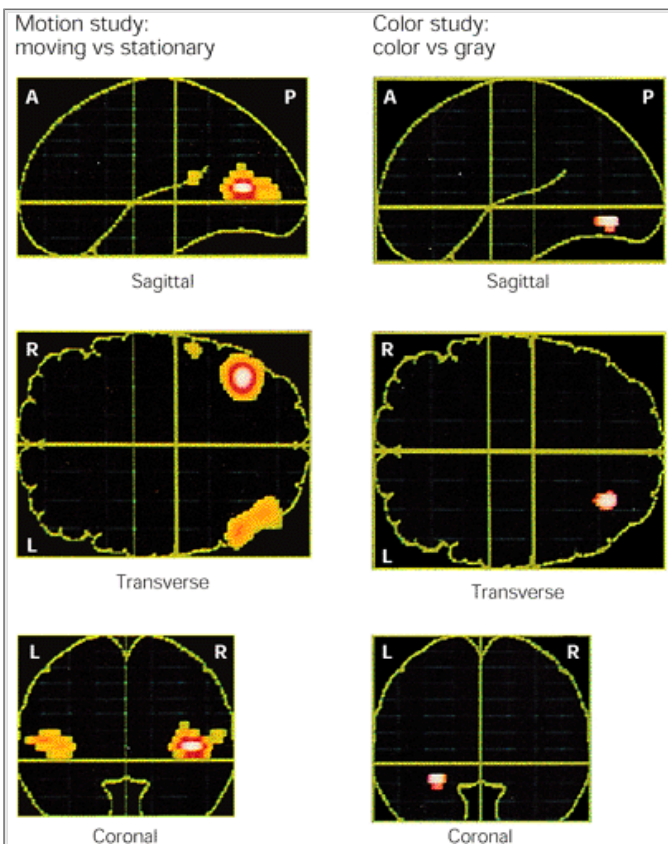


Figure 28-5 Separate human brain areas are activated by motion and color. Motion studies. Six subjects viewed a black and white random-dot pattern that moved in one of eight directions or remained stationary. The figure shows the effect of motion because the PET scans taken while the pattern was stationary were subtracted from those taken while the pattern was moving. The **white** and **red areas** show the high end of activity (increased blood flow). The areas are located on the convexity of the prestriate cortex at the junction of Brodmann's areas 19 and 37.

Color studies. The subjects viewed a collage of 15 squares and rectangles of different colors or, alternatively, the same patterns in gray shades only. The figure shows the difference in blood flow while viewing the color and gray patterns. The area showing increased flow, subserving the perception of color, is located inferiorly and medially in the occipital cortex. (From Zeki et al. 1991).

What should we conclude about the organization of visual processing throughout the multiple areas of the visual cortex? First, we know that there are specific serial pathways through the multiple visual areas, not just a random assortment of equally connected areas. There is substantial evidence for two major processing pathways, a dorsal one to the posterior parietal cortex and a ventral one to the inferior temporal cortex, but other pathways may also exist. Second, there is strong evidence that the processing in these two cortical pathways is hierarchical. Each level has strong projections to the next level (and projections back), and the type of visual processing changes systematically from one level to the next. Third, the functions of cortical areas in the two cortical pathways are strikingly different, as judged both by the anatomical connections and the cellular activity considered in this chapter and by the behavioral and brain imaging evidence discussed in [Chapter 25](#).

Our examination of the functional organization within these vast regions of extrastriate visual cortex begins with the dorsal cortical pathway and the most intensively studied visual attribute, motion. We then examine the processing of depth information in the dorsal pathway. Finally, we turn to the ventral cortical pathway and consider the processing of information related to form. Color vision is the subject of the next chapter.

Motion Is Analyzed Primarily in the Dorsal Pathway to the Parietal Cortex

We usually think of motion as an object moving in the visual field, a car or a tennis ball, and we easily distinguish these moving objects from the stationary background. However, we often see objects in motion not because they move on our retina, but because we track them with eye movements; the image remains stationary on the retina but we perceive movement because our eyes move ([Figure 28-3](#)).

Motion in the visual field is detected by comparing the position of images recorded at different times. Since most cells in the visual system are exquisitely sensitive to retinal position and can resolve events separated in time by 10 to 20 milliseconds, most cells in the visual system should, in principle, be able to extract information about motion from the position of the image on the retina by comparing the previous location of an object with its current location. What then is the evidence for a special neural subsystem specialized for motion?

The initial evidence for a special mechanism designed to detect motion independent of retinal position came from psychophysical observations on *apparent motion*, an illusion of motion that occurs when lights separated in space are turned on and off at appropriate intervals ([Figure 28-4](#)). The perception of motion of objects that in fact have not changed position suggests that position and motion are signaled by separate pathways.

Box 28-1 Optic Flow

Optic flow refers to the perceived motion of the visual field that results from an individual's own movement through the environment. With optic flow the entire visual field moves, in contrast to the local motion of objects. Optic flow provides two types of cues: information about the organization of the environment (near objects will move faster than more distant objects) and information about the control of posture (side-to-side patterns induce body sway). Particularly

influential in the development of ideas about optic flow was the demonstration by the experimental psychologist James J. Gibson that optic flow is critical for indicating the direction of observer movement ("heading"). For example, when an individual moves forward with eyes and head directed straight ahead, optic flow expands outward from a point straight ahead in the visual field, a pattern that is frequently used in movies to show space ship flight.

Where is optic flow represented in the brain? Neurons in one region of the medial superior temporal area of the parietal cortex in monkeys respond in ways that would make these cells ideal candidates to analyze optic flow. These neurons respond selectively to motion, have receptive fields that cover large parts of the visual field, and respond preferentially to large-field motion in the visual field. Additionally, the neurons are sensitive to shifts in the origin of full-field motion and to differences in speed between the center and periphery of the field. The neurons also receive input related to eye movement, which is particularly significant because forward movement is typically accompanied by eye and head movement. Finally, electrical stimulation of this area alters the ability of the monkey to locate the point of origin of field motion, providing further evidence that the superior temporal area of the parietal cortex is important for optic flow.

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Motion Is Represented in the Middle Temporal Area

Experiments on monkeys show that neurons in the retina and lateral geniculate nucleus, as well as many areas in the striate and extrastriate cortex, respond very well to a spot of light moving across their receptive fields. In area V1, however, cells respond to motion in *one* direction, while motion in the opposite direction has little or no effect on them. This *directional selectivity* is prominent among cells in layer 4B of the striate cortex. Thus, cells in the M pathway provide input to cells in 4B, but these input cells themselves do not show directional selectivity. They simply provide the raw input for the directionally selective cortical cells.

In monkeys one area at the edge of the parietal cortex, the middle temporal area (MT), appears to be devoted to motion processing because almost all of the cells are directionally selective and the activity of only a small fraction of these cells is substantially altered by the shape or the color of the moving stimulus. Like V1, MT has a retinotopic map of the contralateral visual field, but the receptive fields of cells within this map are about 10 times wider than those of cells in the striate cortex. Cells with similar directional specificity are organized into vertical columns running from the surface of the cortex to the white matter. Each part of the visual field is represented by a set of columns in which cells respond to different directions of motion in that part of the visual field. This columnar organization is similar to that seen in V1.

Cells in MT respond to motion of spots or bars of light by detecting contrasts in luminance. Some cells in MT also respond to moving forms that are not defined by differences in luminance but by differences only in texture or color. While these cells are not selective for color itself, they nonetheless detect motion by responding to an edge defined by color. Thus, even though MT and the dorsal pathway to the parietal cortex may be devoted to the analysis of motion, the cells are sensitive to stimuli (color) that were thought to be analyzed primarily by cells in the ventral pathway. Stimulus information on motion, form, and color therefore is not processed exclusively in separate functional pathways.

This description of motion processing is based on research on the MT area in monkeys. In the human brain an area devoted to motion has been identified at the junction of the parietal, temporal, and occipital cortices. [Figure 28-5](#) shows changes in blood flow in this area in PET scans made while the subject viewed a pattern of dots in motion.

A cortical area adjacent to MT, the medial superior temporal area (MST), also has neurons that are responsive to visual motion and these neurons may process a type of global motion in the visual field called optic flow, which is important for a person's own movements through an environment ([Box 28-1](#)).

Cells in MT Solve the Aperture Problem

We have considered the response of MT neurons to the motion of simple stimulus like an edge or a line. However,

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in the everyday world complex two- and three-dimensional patterns often give rise to ambiguous or illusory perception. Consider the example in [Figure 28-6A](#), which shows three gratings moving in three directions. When viewed through a small circular aperture, all three gratings appear to move in the same direction. The observer only reports the component of motion that is perpendicular to the orientation of the bars in the gratings. This phenomenon, known as the *aperture problem*, applies to the study of neurons as well as perception. Since most neurons in V1 and MT have relatively small receptive fields, they confront the aperture problem when an object larger than their receptive field moves across the visual field.

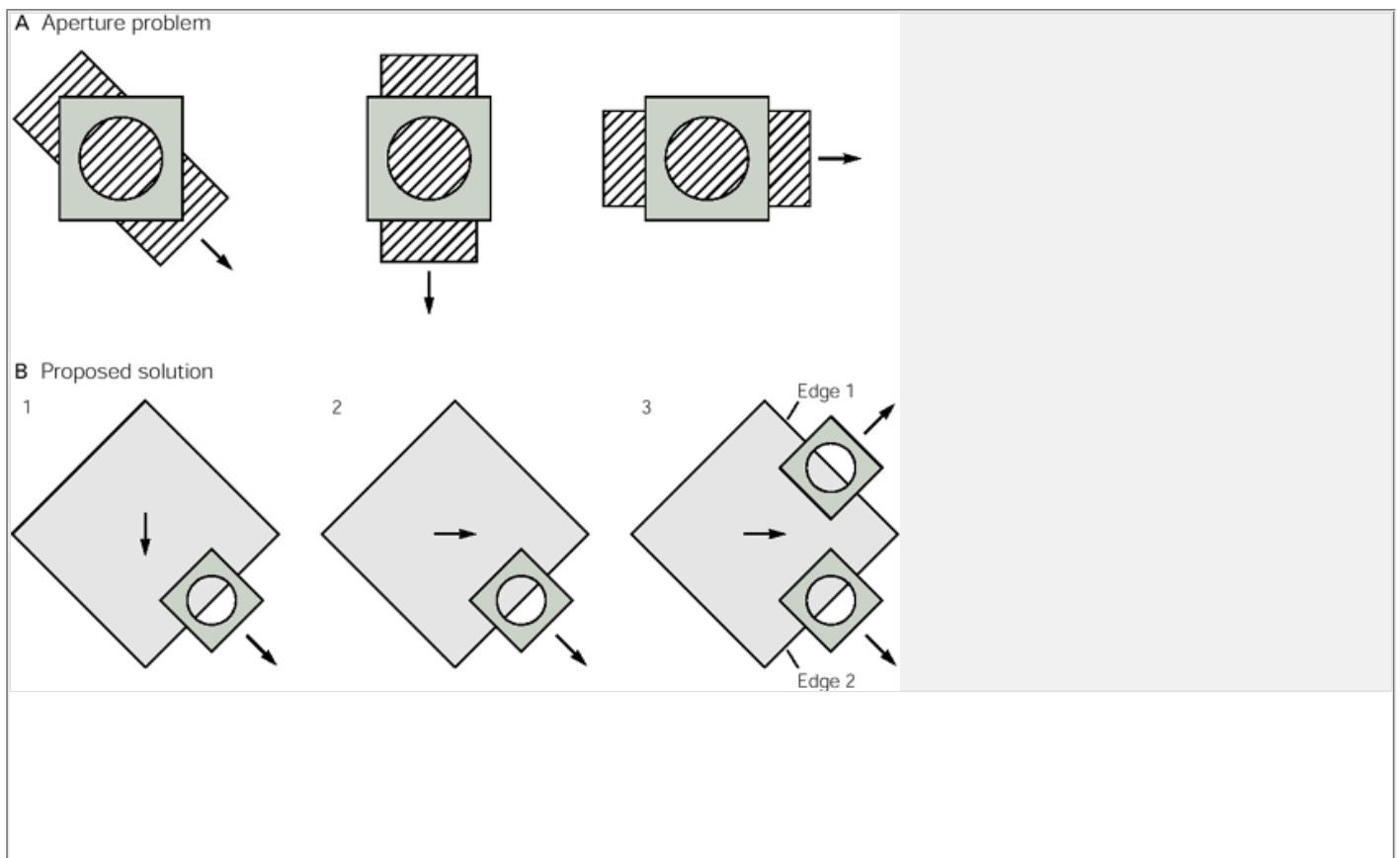


Figure 28-6 The aperture problem.

A. Three patterns moving in three different directions produce the same physical stimulus if only part of the pattern is within view, and thus all three patterns are perceived as moving in the same direction. Three patterns are shown moving in three directions. When seen through a small aperture the three gratings appear to move in the same direction, downward and to the right. This failure to accurately detect the true direction of motion is called the aperture problem. (Adapted from Movshon et al. 1985.)

B. A formal solution to the aperture problem. When motion in different directions, downward (1) or rightward (2), is seen through a small aperture, the motion of the edge seen through the aperture does not indicate the true direction of the entire pattern. Assume now that the aperture represents the receptive field of a neuron, and that there are two apertures rather than one (3). This represents the situation in which two or more cells that respond to specific directions perpendicular to their axis of orientation are activated by different edges moving in different directions. A higher-order cell that integrates the signals from the lower-order cells could encode the motion of the entire object. (Adapted from Movshon 1990.)

To solve the aperture problem, neurons may extract information about motion in the visual field in two stages. In the initial stage neurons that respond to a specific axis of orientation signal motion of components perpendicular to their axis of orientation. The second stage is concerned with establishing the direction of motion of the entire pattern. In this stage higher-order neurons integrate the local components of motion analyzed by neurons in the initial stage.

The hypothesis that motion information in the visual system is processed in two stages was tested by Tony Movshon and his colleagues, who recorded the responses of cells in V1 and MT to a moving plaid pattern. The neurons of V1 as well as the majority of neurons in MT responded only to the components of the plaid. Each cell responded best when the lines in the plaid moved in the direction preferred by the cell. Cells did not respond to the direction of motion of the entire plaid. Movshon therefore called these neurons *component direction-selective neurons*. In contrast, about 20% of the neurons in MT responded only to motion of the plaid pattern. These cells, called **pattern direction-**

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sensitive neurons, receive input from the component direction-selective cells (Figure 28-7). Thus, as suggested by the two-stage hypothesis, the *global motion* of an object is computed by pattern-selective neurons in MT based on the inputs of the component direction-selective neurons in V1 and MT.

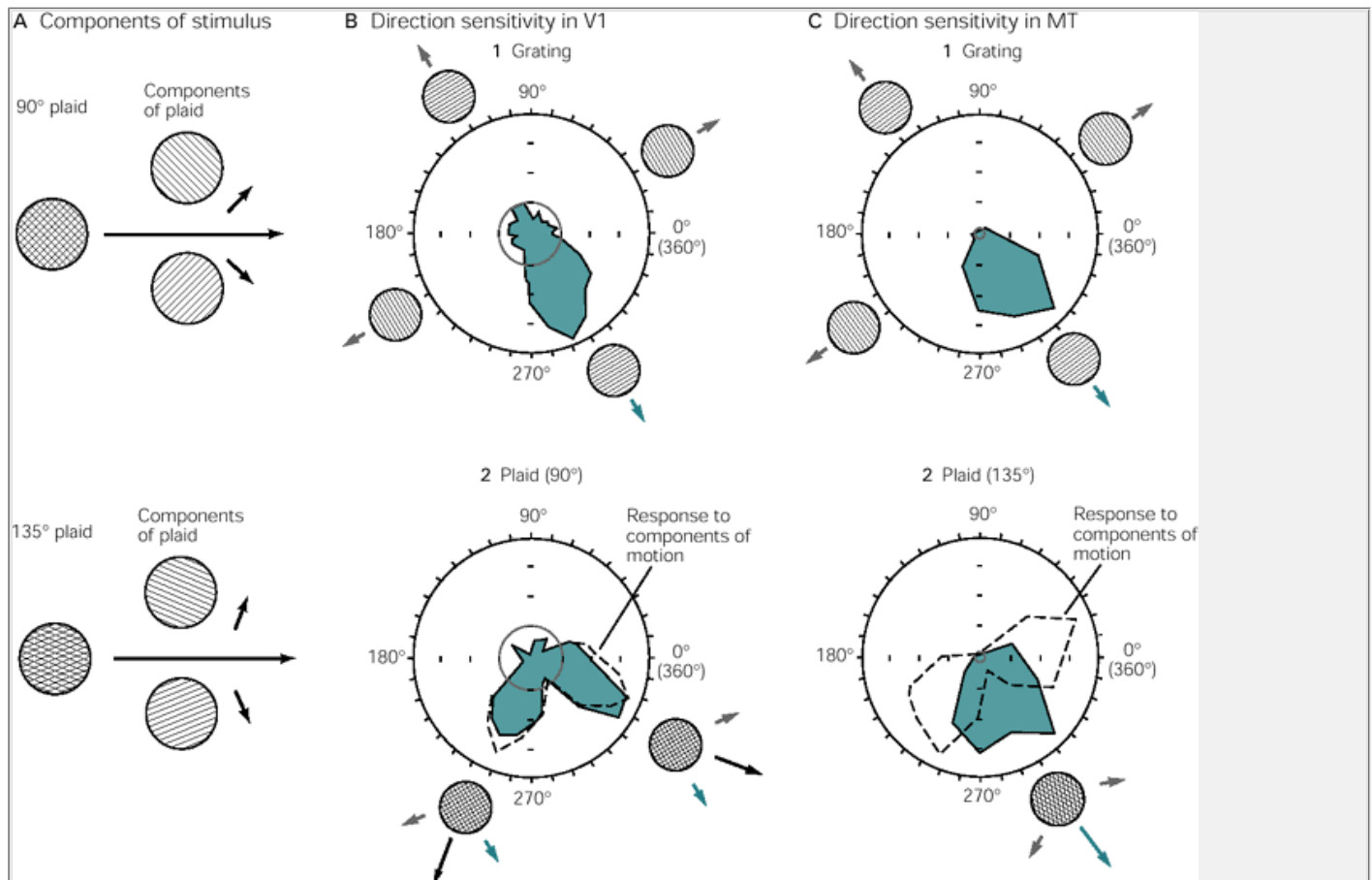


Figure 28-7 Neurons in the middle temporal area of cortex in monkeys are sensitive to the motion of an entire object in the visual field.

A. Stimuli used to activate cells in V1 and MT. Pairs of gratings are oriented at a 90° angle (left) or 135° angle (right) to each other. When each pair is superimposed during movement, the resulting plaid pattern appears to move directly to the right. The motion of each component grating is perpendicular to the orientation of its bars. The movement of either component alone should stimulate first-stage neurons that prefer the direction of motion of the one grating. When the two gratings are superimposed to form a moving plaid, other (second-stage) neurons should be activated.

B. Polar plots illustrate the motion signaled by first-stage neurons in V1. The plots show the response of a neuron to the direction (0 to 360°) of motion of individual gratings (1) and the plaid (2). The response of the neuron to motion in each direction is indicated by the distance of the point from the center of the plot. The circle at the center indicates the neuron's activity when no stimulus is presented.

1. This neuron responds best when the motion of a grating is downward and to the right (**blue arrow**).

2. When presented with the moving plaid, the neuron responds to the motion of each component grating (**solid color**) rather than to the rightward motion of the plaid. The response of the cell to the grating components is expected to have the two-lobed configuration indicated by the **dashed lines**. Neurons that respond only to the motion of the components of the plaid are referred to as component direction-selective neurons.

C. These polar plots illustrate the motion signaled by a higher-order neuron in the middle temporal area (MT).

1. As with the lower-order cell in V1, this cell in MT responds to motion downward and to the right.

2. When presented with the plaid, the neuron responds to the direction of motion of the plaid (**solid color**), not to the directions of the component gratings

(dashed line). This indicates that the neuron has processed the component signals of V1 into a more accurate perception of the movement of the object, and the neuron is referred to as a pattern direction-sensitive neuron. (Modified from Movshon et al. 1985.)

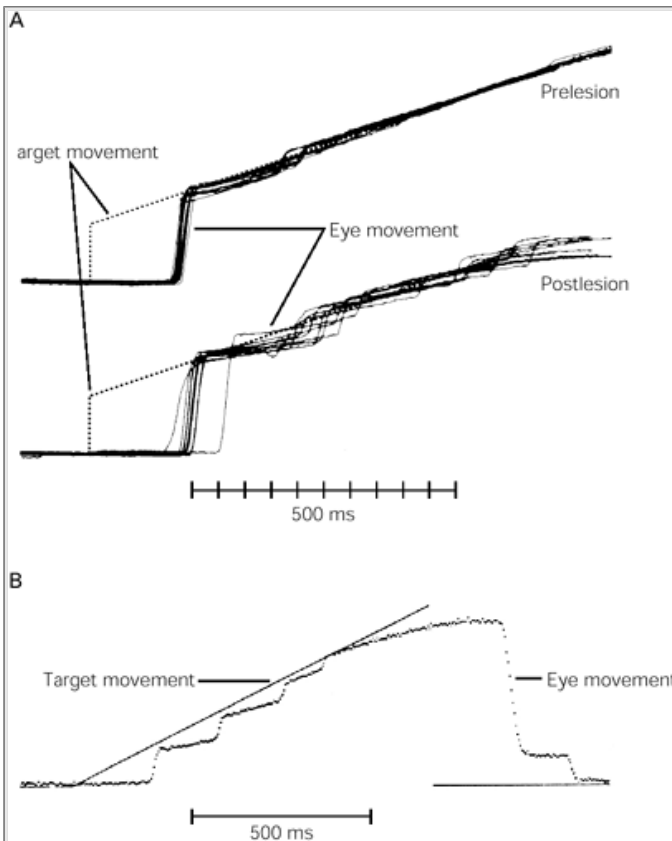


Figure 28-8 Cortical lesions in monkeys and humans produce similar deficits in smooth-pursuit eye movement.

A. Smooth-pursuit eye movements of a monkey before a lesion in the foveal region medial superior temporal area (MST) in the right hemisphere (**prelesion**) and 24 h after the lesion (**postlesion**). The monkey's task is to keep the moving target on the fovea by making smooth-pursuit eye movement. The **dotted line** shows the position of the target over time. The stimulus is turned off where the monkey is fixating and then turned on again as it moves smoothly at 15° per second to the right. The **solid lines** show superimposed eye movements as the monkey pursues the target on 10 separate trials. Note that before the lesion the monkey nearly matches the target motion with smooth-pursuit eye movement, but after the lesion it fails to do so. Instead it makes frequent saccadic eye movements (the series of small steps in the eye movement record) to catch up with the target. (From Dursteler et al. 1987.)

B. Smooth-pursuit eye movements in a human subject with a right occipital-parietal lesion. The patient attempts to follow a target moving 20° per second to the right, but the eye movements do not keep up with the target motion. As with the monkey, the subject uses a series of catch-up saccades to compensate for the slow pursuit. In both humans and monkeys the pursuit deficit is most prominent when the target is moving toward the side of the brain containing the lesion (in these cases, right brain lesions and deficits with rightward pursuit). The human subject, with a large lesion that must include multiple brain areas, has a deficit in smooth-pursuit eye movements very similar to the deficit seen in the monkey with a lesion limited to small and identified visual areas. (From Morrow and Sharpe 1993.)

Control of Movement Is Selectively Impaired by Lesions of MT

These correlations of neuronal activity and visual perception raise the question, Is the activity of direction-selective cells in MT causally related to the visual perception of motion and the control of motion-dependent movement? The question whether direction-selective cells in MT directly affect the control of movement was first addressed in an experiment that examined the relationship of these cells to smooth-pursuit eye movements, the movements that keep a moving target in the fovea (see Figure 28-3). When discrete focal chemical lesions were made within different regions of the retinotopic map in MT of a monkey, the speed of the moving target could no longer be estimated correctly in the region of the visual field monitored by the damaged MT area. In contrast, the lesions did not affect pursuit of targets in other regions of the visual field nor did they affect eye movements to stationary targets. Thus, visual processing in MT is selective for motion of the visual stimulus; lesions produce a blind spot, or a scotoma, for motion.

Human patients with lesions of parietal cortex also sometimes have these deficits in smooth-pursuit eye movements, but the most frequent behavioral deficit is quite different from that seen after lesions of MT. The neurologist Gordon Holmes originally reported that these patients were unable to follow a target when it was moving toward the side of the brain that had the lesion. For example, a patient with a lesioned right hemisphere has difficulty pursuing a target moving toward the right (Figure 28-8B). Later experiments on monkeys showed that lesions centered on the medial superior temporal area (MST), the next level of processing for visual motion, produced just such a deficit (Figure 28-8A).

Perception of Motion Is Altered by Lesions and Microstimulation of MT

The question whether MT cells contribute to the perception of visual motion was addressed in an experiment in which monkeys were trained to report the direction of motion in a display of moving dots. The experimenter varied the proportion of dots that moved in the same direction. At zero correlation the motion of all dots was

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random and at 100% correlation the motion of all dots was in one direction (Figure 28-9A). While normal monkeys could perform the task with less than 10% of the dots moving in the same direction, monkeys with a lesion in MT required nearly 100% coherence to perform as well (Figure 28-9B). A human patient with bilateral brain damage also lost the perception of motion when tested on the same task (Figure 28-9B). In both the monkeys and the human subject, visual acuity for stationary stimuli was not affected by the brain damage.

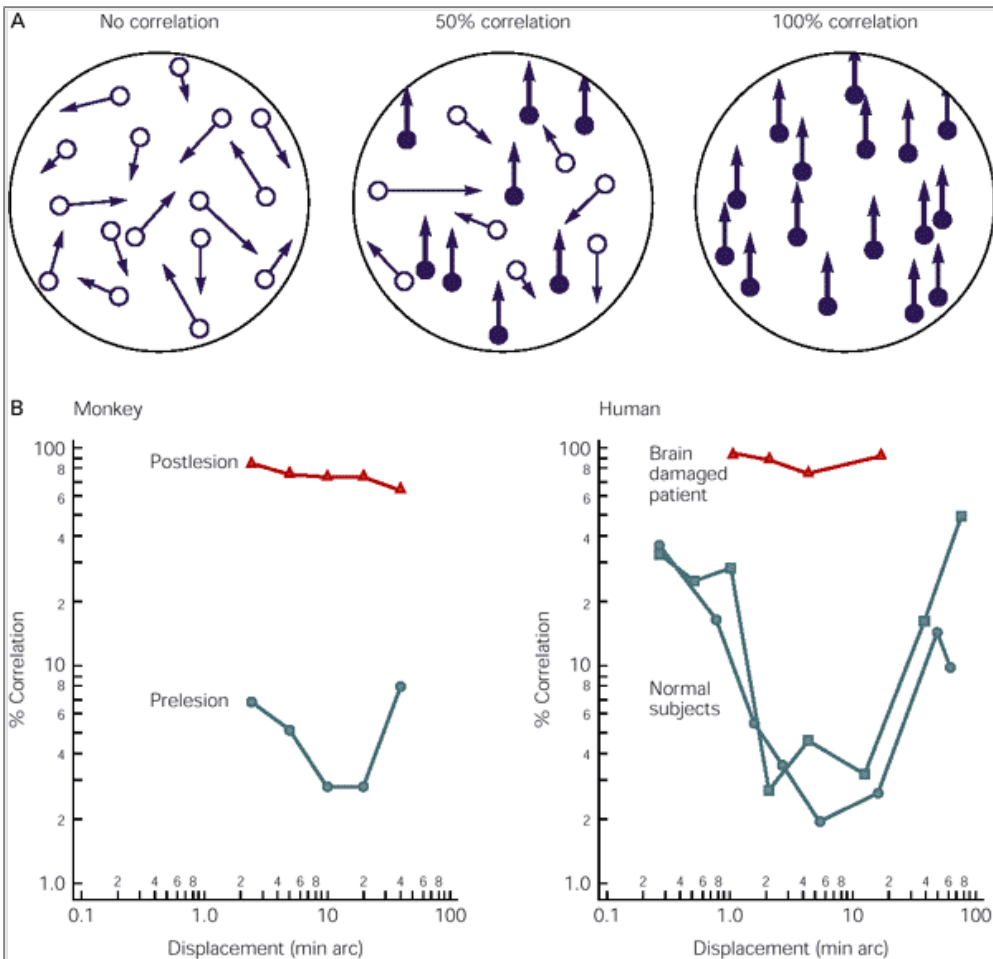


Figure 28-9 A monkey with an MT lesion and a human patient with damage to extrastriate visual cortex have similar deficits in motion perception.

A. Displays used to study the perception of motion. In the display on the left there is no correlation between the directions of movement of several dots, and thus no net motion in the display. In the display on the right all the dots move in the same direction (100% correlation). An intermediate case is in the center; 50% of the dots move in the same direction while the other 50% move in random directions (essentially noise added to the signal). (From [Newsome and Pare 1988](#).)

B. The performance of a monkey before and after an MT lesion (**left**). The performance of a human subject with bilateral brain damage is compared to two normal subjects (**right**). The ordinate of the graph shows the percent correlation in the directions of all moving dots (as in part A) required for the monkey to pick out the one common direction. The abscissa indicates the size of the displacement of the dot and thus the degree of apparent motion. Note the general similarity between the performance of the humans and that of the monkey and the devastation to this performance after the cortical lesions. (From [Newsome and Pare 1988](#), [Baker et al. 1991](#).)

Thus damage to MT reduces the ability of monkeys to detect motion in the visual field, as indicated by disruptions in the pursuit of moving objects and perception of the direction of motion. However, monkeys with MT lesions quickly recover these functions. Directionally selective cells in other areas of cerebral cortex, such as MST, apparently can take over the function performed by MT. Recovery of function is greatly slowed when the lesion affects not only MT but also MST and other extrastriate areas.

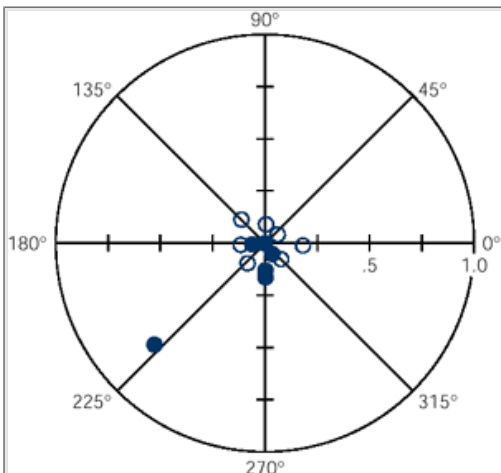


Figure 28-10 Alteration of perceived direction of motion by stimulation of MT neurons. A monkey was shown a display of moving dots with a relatively low correlation of 25.6% (see [Figure 28-9A](#)) and instructed to indicate in which of eight directions the dots appeared to be moving. The **open circles** show the proportion of decisions made for each direction of motion—about equal choice for all directions. Electric current was passed through a microelectrode positioned among cells that responded best to stimulus motion in one direction, 225° on the polar plot. The microstimulation was applied for 1 s, beginning and ending with the onset and offset of the visual stimulus. **Filled circles** show the response of the monkey when the MT cells were stimulated at the same time the visual stimulus was presented. Stimulation increased the likelihood that the monkey would indicate seeing motion in the direction preferred by the stimulated MT cells (225°). (Adapted from [Salzman and Newsome 1994](#).)

If cells in MT are directly involved in the analysis of motion, the firing patterns of these neurons should affect perceptual judgments about motion. How well does the firing pattern of these neurons actually correlate with behavior? To address this question, William Newsome and Movshon recorded the activity of direction-selective neurons in MT while the monkeys reported the direction of motion in a random-dot display. Firing of the neurons correlated extremely well with performance. Thus the directional information encoded by the neurons of MT cells is sufficient to account for the monkey's judgment of motion.

If this inference is correct, then modifying the firing rates of the MT neurons should alter the monkey's perception of motion. In fact, Newsome found that stimulating clusters of neurons in a single column of cells sensitive to one direction of motion biases the monkey's judgment toward that direction of motion. The electrical stimulation acts as if a constant visual motion signal were added to the signal conveyed by the whole population of MT neurons (Figure 28-10). Thus, the firing of a relatively small population of motion-sensitive neurons in MT directly contributes to perception.

Depth Vision Depends on Monocular Cues and Binocular Disparity

One of the major tasks of the visual system is to convert a two-dimensional retinal image into three dimensions. How is this transformation achieved? How do we tell how far one thing is from another? How do we estimate the relative depth of a three-dimensional object in the visual field? Psychophysical studies indicate that the shift from two to three dimensions relies on two types of clues: monocular cues for depth and stereoscopic cues for binocular disparity.

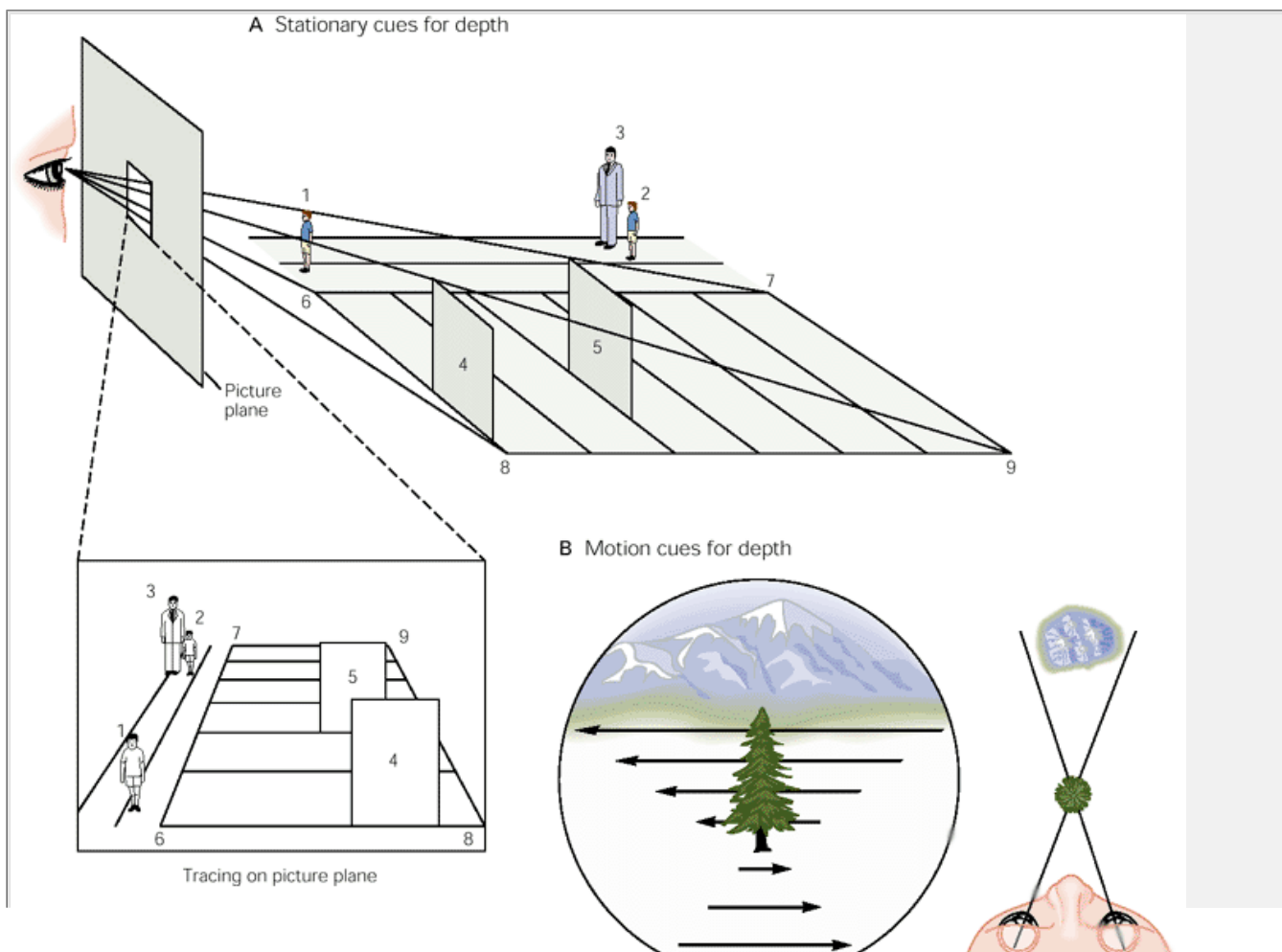
Monocular Cues Create Far-Field Depth Perception

At distances greater than about 100 feet the retinal images seen by each eye are almost identical, so that looking at a distance we are essentially one-eyed. Nevertheless we can perceive depth with one eye by relying on a variety of tricks called monocular depth cues. Several of these monocular cues were appreciated by the artists of antiquity, rediscovered during the Renaissance, and codified early in the sixteenth century by Leonardo da Vinci.

- *Familiar size.* If we know from experience something about the size of a person, we can judge the person's distance (Figure 28-11A).
- *Occlusion.* If one person is partly hiding another person, we assume the person in front is closer (Figure 28-11A).
- *Linear perspective.* Parallel lines, such as those of a railroad track, appear to converge with distance. The greater the convergence of lines, the greater is the impression of distance. The visual system interprets the convergence as depth by assuming that parallel lines remain parallel (Figure 28-11A).
- *Size perspective.* If two similar objects appear different in size, the smaller is assumed to be more distant (Figure 28-11A).
- *Distribution of shadows and illumination.* Patterns of light and dark can give the impression of depth. For example, brighter shades of colors tend to be seen as nearer. In painting this distribution of light and shadow is called *chiaroscuro*.

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- *Motion (or monocular movement) parallax.* Perhaps the most important of the monocular cues, this is not a static pictorial cue and therefore does not come to us from the study of painting. As we move our heads or bodies from side to side, the images projected by an object in the visual field move across the retina. Objects closer than the object we are looking at seem to move quickly and in the direction opposite to our own movement, whereas more distant objects move more slowly and in the same direction as our movement (Figure 28-11B).



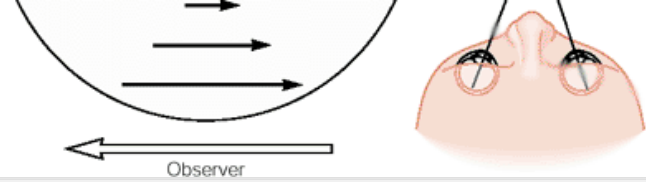


Figure 28-11 Monocular depth cues provide information on the relative distance of objects and have been used by painters since antiquity.

A. The upper drawing shows the side view of a scene. When the scene is traced on a plane of glass held between the eye and the scene (lower drawing) the resulting two-dimensional tracing reveals the cues needed to perceive depth. **Occlusion:** The fact that rectangle 4 interrupts the outline of 5 indicates which object is in front, but not how much distance there is between them. **Linear perspective:** Although lines 6-7 and 8-9 are parallel in reality, they converge in the picture plane. **Size perspective:** Because the two boys are similar figures, the smaller boy (2) is assumed to be more distant than the larger boy (1) in the picture plane. **Familiar size:** The man (3) and the nearest boy are drawn to nearly the same size in the picture. If we know that the man is taller than the boy, we deduce on the basis of their sizes in the picture that the man is more distant than the boy. This type of cue is weaker than the others. (Adapted from Hochberg 1968.)

B. Motion of the observer or sideways movement of head and eyes produces depth cues. If the observer moves to the left while looking at the tree, objects closer than the tree move to the right; those farther away move to the left. The full-field motion that results from the observer's own movement is referred to as optic flow. (see [Box 28-1](#).) (Adapted from [Busetini et al. 1996](#)).

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Stereoscopic Cues Create Near-Field Depth Perception

The perception of depth at distances less than 100 feet also depends on monocular cues but in addition is mediated by stereoscopic vision. Stereoscopic vision is possible because the two eyes are horizontally separated (by about 6 cm in humans) so that each eye views the world from a slightly different position. Thus, objects at different distances produce slightly different images on the two retinas. This can be clearly demonstrated by closing each eye in turn. As vision is switched from one to the other eye, any near object will appear to shift sideways.

Understanding stereopsis begins with an understanding of the simple geometry of the images falling on the retina. When we fixate on a point, the image of this point falls upon corresponding points on the center of the retina in each eye ([Figure 28-12](#)). The point of focus is called the *fixation point*; the parallel (vertical) plane of points on which it lies is called the *fixation plane*. The distance of an image from the center of the two eyes allows the visual system to calculate the distance of the object relative to the fixation point. Any point on the object that is nearer or farther than the fixation point will project an image at some distance from the center of the retina. Parts of the object that are closer to us will be farther apart on the two retinas in a horizontal direction. Parts of the object that are farther from us will project closer together on the two retinas.

Clearly, the difference in position, called *binocular disparity*, depends on the distance of the object from the fixation plane. Thus points on a three-dimensional object just outside the fixation plane stimulate different points on each eye, and the multiple disparities provide cues for stereopsis, the perception of solid objects.

Surprisingly, not one of the great early students of optics—Euclid, Archimedes, Leonardo da Vinci, Newton, nor Goethe—understood stereopsis, although each could readily have discovered it with the methods available to them. Stereoscopic vision was not discovered until 1838, when the physicist Charles Wheatstone invented the stereoscope. Two photographs of a scene 60-65 mm apart, one taken from the position of each eye, are mounted into a binocular-like device such that the right eye sees only the picture taken from one position and the left eye sees only the other picture. Remarkably, this presentation produces a three-dimensional scene.

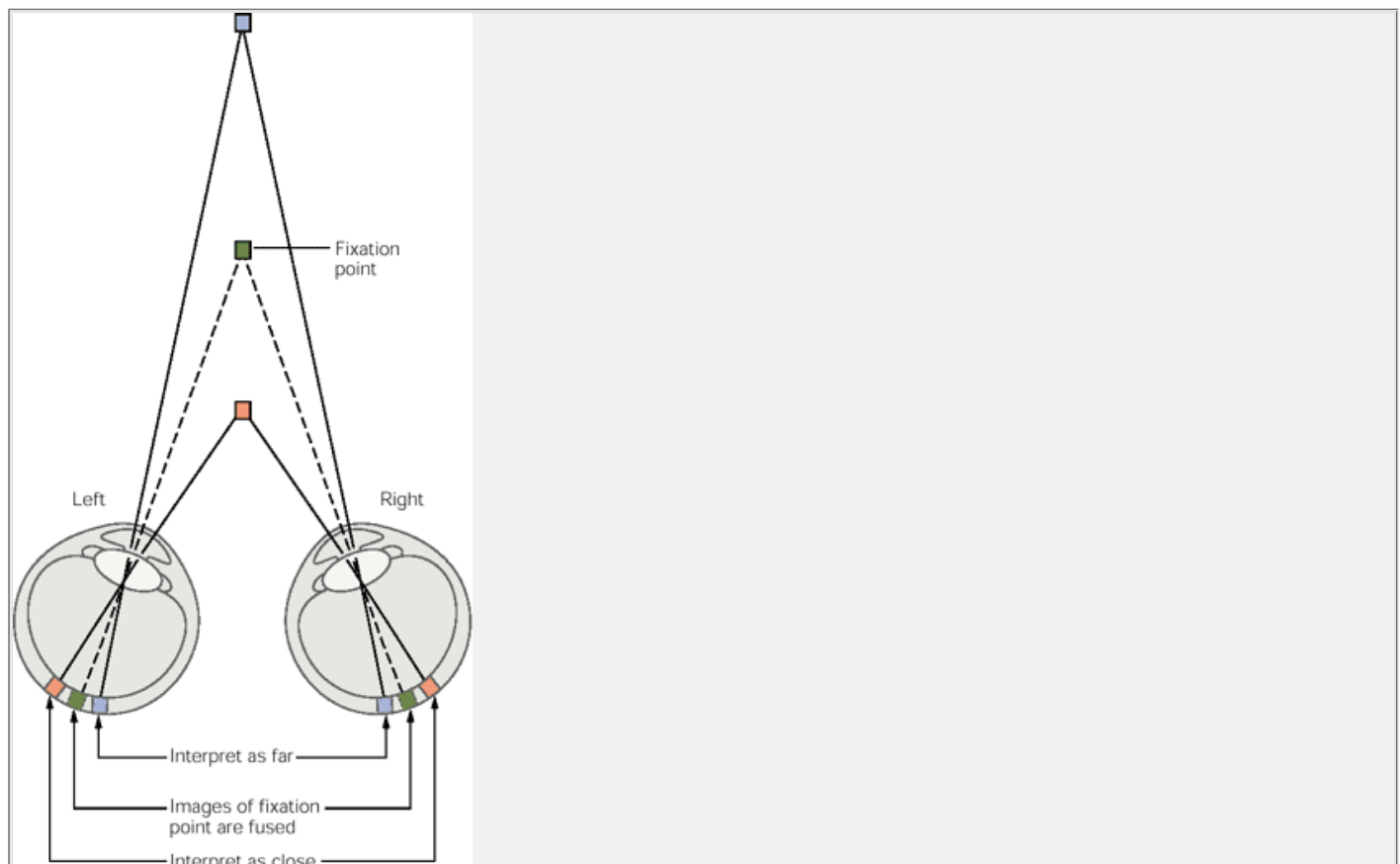


Figure 28-12 When we fix our eyes on a point the convergence of the eyes causes that point (the fixation point) to fall on identical portions of each retina. Cues for depth are provided by points just proximal or distal to the fixation point. These points produce binocular disparity by stimulating slightly different parts of the retina of each eye. When the lack of correspondence is in the horizontal direction only and is not greater than about 0.6 mm or 2° of arc, the disparity is perceived as a single, solid (three-dimensional) spot.

Information From the Two Eyes Is First Combined in the Primary Visual Cortex

How is stereopsis accomplished? Clearly the brain must somehow calculate the disparity between the images seen by the two eyes and then estimate distance based on simple geometric relations. However, this cannot occur before information from the two eyes comes together, and cells in the primary visual cortex (V1) are the first in the visual system to receive input from the two eyes ([Chapter 27](#)). Stereopsis, however, requires that the inputs from the two eyes be slightly *different*—there must be a horizontal disparity in the two retinal images ([Figure 28-13](#)). The important finding that certain neurons in V1 are actually selective for horizontal disparity was

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made in 1968 by Horace Barlow, Colin Blakemore, Peter Bishop, and Jack Pettigrew. They found that a neuron that prefers an oriented bar of light at one place in the visual field responds better when that stimulus appears in front of the screen (referred to as a near stimulus) or when the stimulus is beyond the screen (a far stimulus). There is thus an additional level of organization of information in the ocular dominance columns in V1.

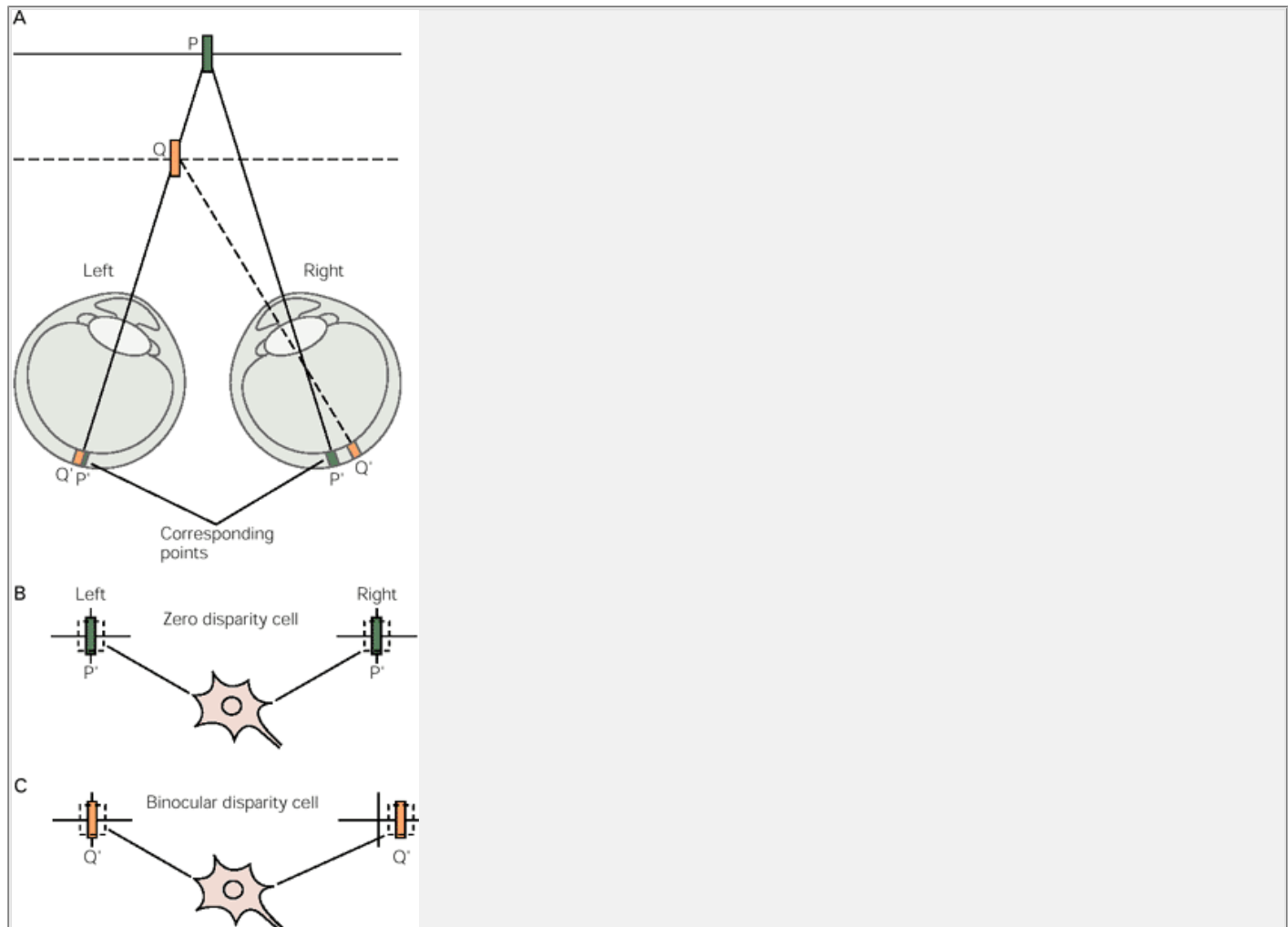


Figure 28-13 Neuronal basis of stereoscopic vision. (Adapted from [Ohzawa et al. 1996](#).)

A. When an observer looks at point P the image P' falls on corresponding points on the retina of each eye. These images completely overlap and therefore have zero binocular disparity. When looking at a point to the left and closer, point Q, the image Q' in the left eye falls on the same point as P', but the image in the right eye is laterally displaced. These images have binocular disparity.

B. A cortical neuron receiving binocular inputs is maximally activated when the inputs from the two eyes have zero disparity as at P'.

C. Another cortical neuron receiving binocular inputs responds best when the inputs from the two eyes are spatially disparate on the two retinas (Q'); it is most sensitive to near stimuli.

Cells sensitive to binocular disparity are found in several cortical visual areas. In addition to V1, some cells in the extrastriate areas V2 and V3 respond to disparity, and many direction-selective cells in MT respond best to stimuli at specific distances, either at the plane of fixation or nearer or farther than the plane. Some cells in MST, the next step in the parietal pathway, fire in response to combinations of disparity and direction of motion. That is, the direction of motion preferred by the cell varies with the disparity of the stimulus. For example, a cell that responds to leftward-moving far stimuli might also respond to rightward-moving near stimuli. These cells can convey information not only about the direction of motion but about the direction of motion at different depths within the visual field (as in [Figure 28-11B](#)).

Studies of cells in the striate and extrastriate cortex that respond selectively to binocular disparity fall into several broad categories. Among these, tuned cells respond best to stimuli at a specific disparity, frequently on the plane of fixation. Other cells respond best to stimuli at a range of disparities either in front of the fixation plane ("near cells") or beyond the plane ("far cells") ([Figure 28-14](#)).

Just as the motion information processed in MT is used both for the visual guidance of movement and for visual perception, disparity-sensitive cells in different regions of visual cortex may use disparity information for different purposes. One use is the perception of depth, which we have already considered. Another is in aligning the eyes to focus at a particular depth in the field. The eyes rotate toward each other (convergence) to focus on near objects and rotate apart (divergence) to focus on more distant objects. The ability to align the eyes develops in the first few months of life and disparity information may play a key role in establishing this alignment.

Random Dot Stereograms Separate Stereopsis From Object Vision

Must the brain recognize an object before it can match the corresponding points of the object in the two eyes? Until 1960 this was generally thought to be so, and stereopsis therefore was thought to be a late stage in visual processing. In 1960 Bela Julesz proved that this idea was wrong when he found that stereoscopic fusion and depth perception do not require monocular identification of form. The only clue necessary for stereopsis is retinal disparity.

To demonstrate this remarkable fact, Julesz created a pattern of randomly distributed dots in the middle of which is a square area of dots. He made two copies of P.562

the pattern but in one copy the inner square of dots is positioned slightly differently from the other copy. The inner square of dots is visible only when the identical copies of the pattern are viewed in a stereoscope. If one inner square is displaced so the two squares are closer together, in binocular view the square appears to lie in front of the pattern. If one inner square is shifted so the two squares are further apart, the perceived square appears to lie behind the surrounding dots (Figure 28-15). By itself, each random-dot pattern will not produce any depth clues. Only with stereoscopic vision can one see the square within the pattern. With this method, Julesz demonstrated that humans can detect form based strictly on binocular disparity.

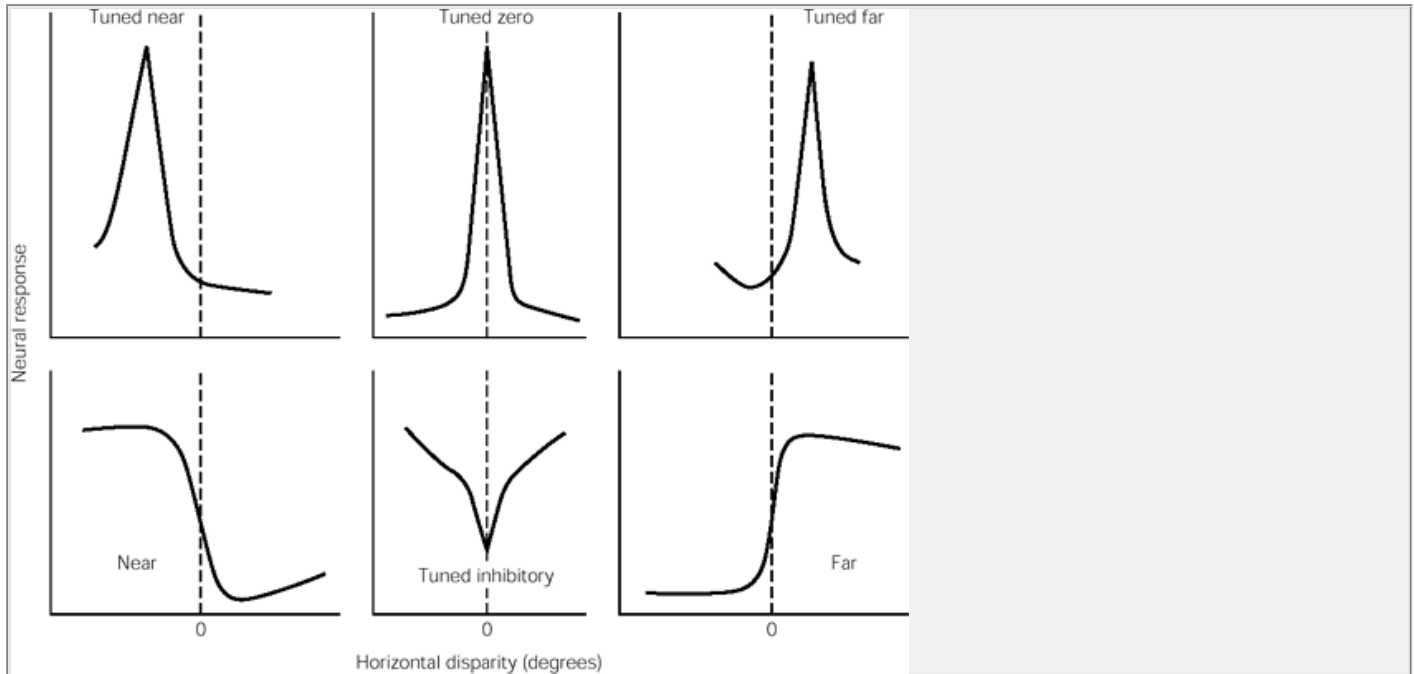


Figure 28-14 Different disparity profiles are found in neurons in cortical visual areas of the monkey. The curves show the responses of six different neurons to bright bars of optimal orientation moving in the preferred direction across the receptive fields at a series of horizontal disparities. These different disparity profiles have been observed in many areas of the monkey visual cortex. The tuned cells are more common in areas V1 and V2, especially in the region of foveal representation, and the "near" and "far" cells are more common in MST. (After Poggio 1995.)

Are there, among the disparity-sensitive neurons in the visual cortex, individual neurons that respond to a stereogram that contains no depth clues except retinal disparity? To answer this question, Gian Poggio first located responsive cells using a bar of light as a stimulus. He then replaced the bar with a random-dot pattern stereogram. Many of the neurons that responded to the solid figure also responded to the random-dot stereogram.

Object Vision Depends on the Ventral Pathway to the Inferior Temporal Lobe

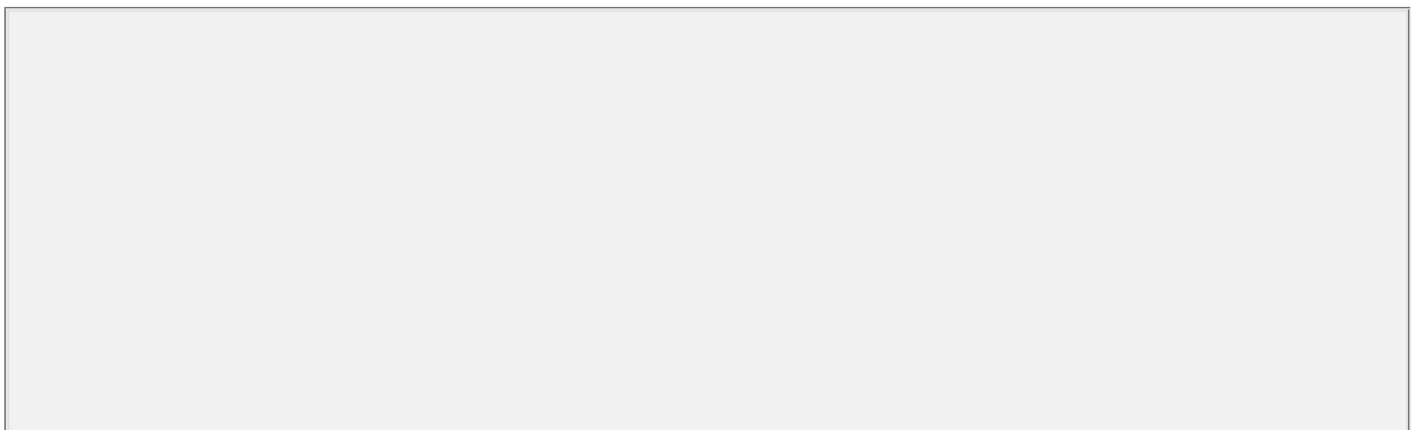
The ventral cortical pathway extends from V1 through V2 to V4 and then to the inferior temporal cortex. We have already noted that V2 has subregions referred to as thick stripes, thin stripes, and interstripes and that the thin and interstripe regions project to V4. As we have indicated, the ventral pathway appears to be concerned with analysis of form and color. Here we will concentrate on the processing of form in V2, V4, and the inferior temporal cortex.

Cells in V2 Respond to Both Illusory and Actual Contours

As in V1, cells in V2 are sensitive to the orientation of stimuli, to their color, and to their horizontal disparity, and they continue the analysis of contour begun by cells in V1. Their response to contours was explored in experiments in which cells were tested for their sensitivity to certain illusory contours of the sort we considered in Chapter 25.

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Many cells in V2 responded to the illusory contours just as they responded to edges (Figure 28-16). In contrast, few cells in V1 responded to the same illusory contours (although other experiments have shown responses of V1 cells to more limited illusory contours). These results suggest that V2 carries out an analysis of contours at a level beyond that of V1, and they are further evidence of the progressive abstraction that occurs in each of the two pathways of the visual system.



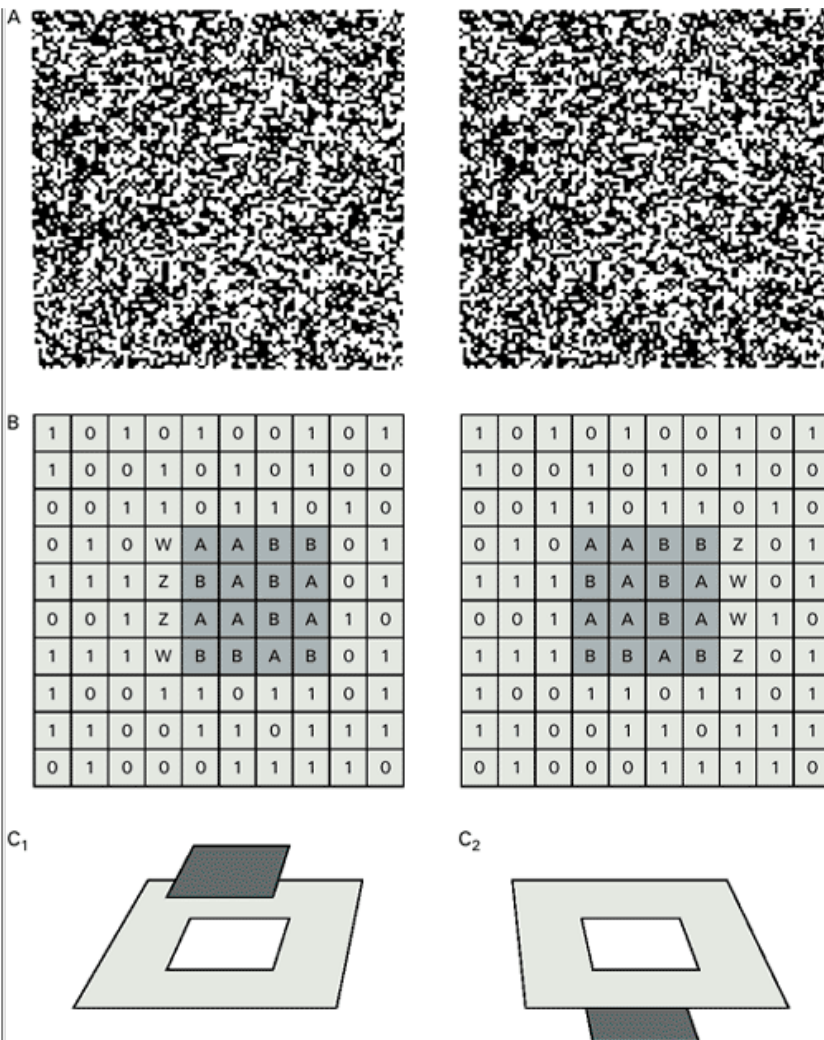


Figure 28-15 Stereopsis does not depend on perception of form.

A. A square form inside these identical random-dot displays cannot be seen by looking at either display alone. It can be seen only when the two identical images are viewed in a stereoscope, or by training the eyes to focus outside the image plane.

B. The square areas in the two random-dot patterns have different positions. The square becomes visible only because of the ocular disparity of the two dot patterns, not because either eye recognizes the form of the square.

C. In the stereoscope the random-dot images are placed behind a rectangular opening. If one inner square of dots is displaced so the left and right inner squares are closer together (**1**), the square is perceived in front of the larger pattern. If the inner squares are shifted so that the two squares are further apart (**2**), the square is perceived behind the larger pattern. (Adapted from [Julesz 1971](#).)

Cells in V4 Respond to Form

Initial observations on cells in V4 indicated that the cells were selective for color, and it was thought that they were devoted exclusively to color vision. However, many of these same cells are also sensitive to the orientation of bars of light and are more responsive to finer-grained than to coarse-grained stimuli. Thus, some V4 cells are responsive to combinations of color and form.

Does removal of V4 alter a monkey's responses to color more than to form? Experiments show that ablation of V4 impairs a monkey's ability to discriminate patterns and shapes but only minimally affects its ability to distinguish colors with different hues and saturation. In other experiments ablation of V4 altered only subtle color discriminations, such as the ability to identify colors under different illumination conditions (*color constancy*).

We have noted that some humans lose color vision (achromatopsia) after localized damage to the ventral occipital cortex. PET scans of normal human subjects reveal

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an increase in activity in the lingual and fusiform gyri when colored stimuli are presented (see [Figure 28-5](#)). The deficits in patients with achromatopsia differ from those in monkeys with lesions of V4. The human patients cannot discriminate hues but can discriminate shape and texture, whereas the monkeys' ability to differentiate shapes is markedly diminished while hue discrimination is only minimally affected. It therefore seems unlikely that the area identified in the human brain is directly comparable to the V4 region in the monkey, but instead includes more extended regions, including the inferior temporal cortex, the area we consider next.

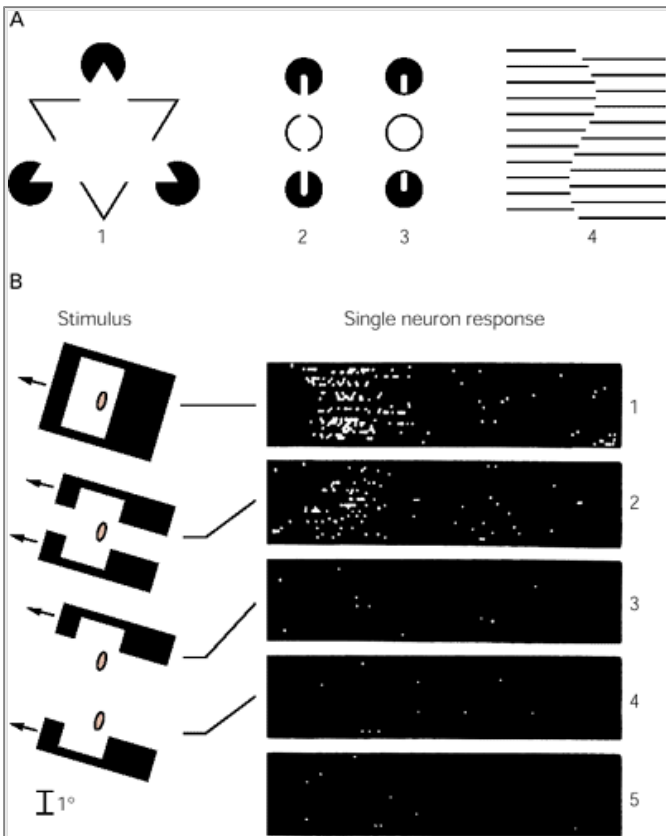


Figure 28-16 Illusions of edges used to study the higher level information processing in V2 cells of the monkey.

A. Examples of illusory contours. **1.** A white triangle is clearly seen, although it is not defined in the picture by a continuous border. **2.** A vertical bar is seen, although again there is no continuous border. **3.** Slight alterations obliterate the perception of the bar seen in **2.** **4.** The curved contour is not represented by any edges or lines. (From [Von der Heydt et al. 1984.](#))

B. A neuron in V2 responds to illusory contours. The cell's receptive field is represented by an ellipse in the drawings on the left. **1.** A cell responds to a bar of light moving across its receptive field. Each dot in the record on the right indicates a cell discharge and successive lines indicate the cell's response to successive movements of the bar. **2.** The neuron also responds when an illusory contour passes over its receptive field. **3, 4.** When only half of the stimulus moves across the cell's receptive field, the response resembles spontaneous activity (**5**). (Adapted from [Von der Heydt et al. 1984.](#))

Recognition of Faces and Other Complex Forms Depends Upon the Inferior Temporal Cortex

We are capable of recognizing and remembering an almost infinite variety of shapes independent of their size or position on the retina. Clinical work in humans and experimental studies in monkeys suggest that form recognition is closely related to processes that occur in the inferior temporal cortex.

The response properties of cells in the inferior temporal cortex are those we might expect from an area involved in a later stage of pattern recognition. For example, the receptive field of virtually every cell includes the foveal region, where fine discriminations are made. Unlike cells in the striate cortex and many other extrastriate visual areas, the cells in the inferior temporal area do not have a clear retinotopic organization, and the receptive fields are very large and occasionally may include the entire visual field (both visual hemifields). Such large fields may be related to *position invariance*, the ability to recognize the same feature anywhere in the visual field. For example, even a small eye movement can easily move an edge stimulus from the receptive field of one V1 neuron to another. In contrast, such a movement would simply move the edge within the receptive field of one inferior temporal neuron. The larger receptive field of many extrastriate regions, including the inferior temporal, may be important in the ability to recognize the same object regardless of its location.

The most prominent visual input to the inferior temporal cortex is from V4, so it would not be surprising to see a continuation of the visual processing observed in V4. Inferior temporal cortex appears to have functional subregions and, like V4, may have separate pathways to these regions. Also like V4, inferior temporal cells are sensitive to both shape and color. Many cells in inferior temporal cortex respond to a variety of shapes and colors, although the strength of the response varies for different combinations of shape and color ([Figure 28-17](#)). Other cells are selective only for shape or color.

Most interesting is the finding that some inferotemporal cells respond only to specific types of complex stimuli, such as the hand or face. For cells that respond to a hand, the individual fingers are a particularly critical visual feature; these cells do not respond when there are no spaces separating the fingers. However, all orientations of the hand elicit similar responses. Among

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neurons selective for faces, the frontal view of the face is the most effective stimulus for some, while for others it is the side view. Moreover, whereas some neurons respond preferentially to faces, others respond preferentially to specific facial expressions. Although the proportion of cells in the inferior temporal cortex responsive to hands or faces is small, their existence, together with the fact that lesions of this region lead to specific deficits in face recognition ([Chapter 25](#)), indicates that the inferior temporal cortex is responsible for face recognition.

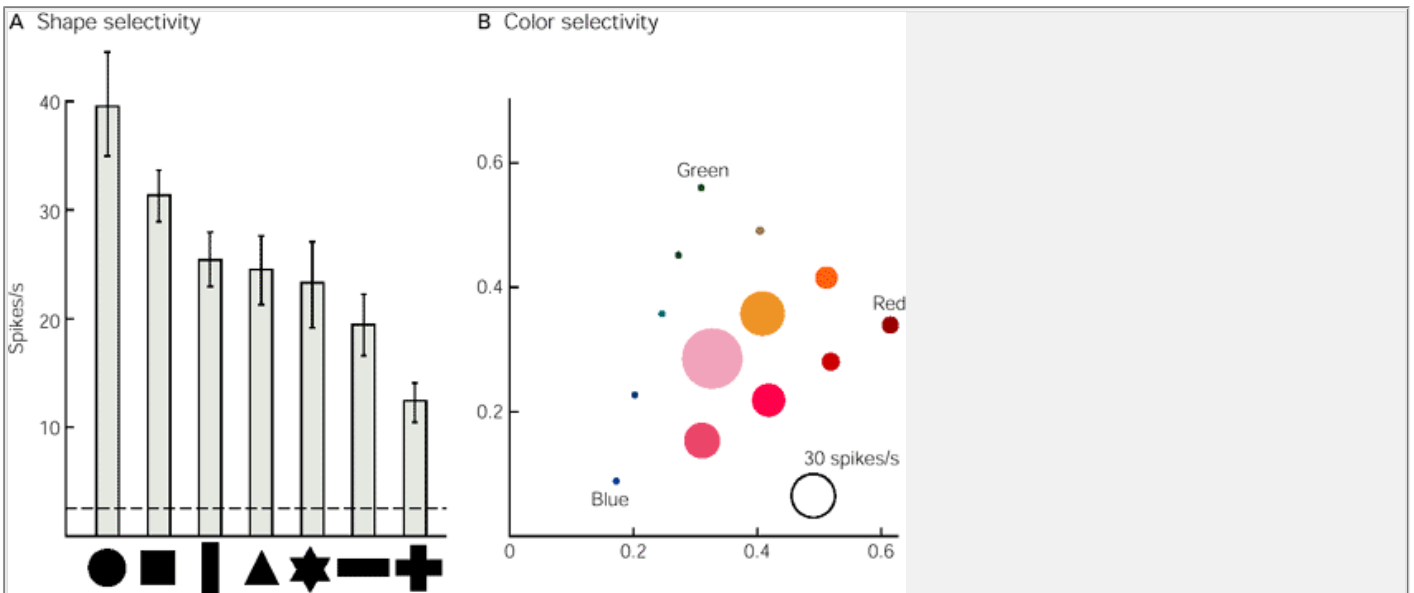


Figure 28-17 Many inferior temporal neurons respond both to form and color.

A. Average responses for a single neuron to stimuli with different shapes. The height of each bar indicates the average discharge rate during presentation of the stimulus. The **dashed line** indicates the background discharge rate.

B. Responses of the same neuron to colored stimuli. Discharge rates are indicated by the size of each circle. The **open circle** represents a discharge rate of 30 spikes/s. The responses are plotted on a color map with the relative location of colors, red, green, and blue given for reference. The axes are relative amounts of primary colors. (Adapted from [Komatsu and Ideura 1993](#).)

One of the major issues in understanding the brain's analysis of complex objects is the degree to which individual cells respond to the simpler components of these objects. Certain critical elements of faces are sufficient to activate some inferior temporal neurons. For example, instead of a face, two dots and a line appropriately positioned might activate the cell ([Figure 28-18](#)). Other experiments suggest that some cells respond to facial dimensions (distance between the eyes) and others to the familiarity of the face. There is also evidence that cells responding to similar features are organized in columns.

Visual Attention Facilitates Coordination Between Separate Visual Pathways

The limited capacity of the visual system means that at any given time only a fraction of the information available from the visual scene falling on the two retinas can be processed. Thus some information is used to produce perception and movement while other information is lost or discarded. This selective filtering of visual information is achieved by visual attention. As may be appreciated from the evidence presented in this and earlier chapters, understanding the neuronal mechanisms of attention and conscious awareness is one of the great unresolved problems in perception. Can we resolve these mechanisms and understand their contribution to behavior? How does attention alter the processing of visual information?

Investigation of spatial attention at the neuronal level began in the 1970s with exploration of the cellular basis of visual attention in the superior colliculus, the striate cortex (V1), and the posterior parietal cortex of awake primates (see [Figure 20-15](#)). Michael Goldberg and Robert Wurtz examined the response of cells to a spot of light under two conditions: (1) when the monkey looked elsewhere and did not attend to the location of the spot, and (2) when the animal was required to fix its gaze on the spot of light by making rapid or saccadic eye movements to the spot. When the animal attended to the spot, cells in the superior colliculus responded more intensely, while the response of cells in V1 showed little modulation. However, the enhanced response of the cells in the superior colliculus did not result from selective attention per se but was dependent upon the initiation of eye movement. In similar tests of the responsiveness of cells in the posterior parietal cortex, a region known from clinical studies to be involved in attention ([Chapter 20](#)), the cells' responses were enhanced whether the monkey made an eye movement to the visual target or reached for it ([Box 28-2](#)).

The effects of attention on cells in V4 and inferior temporal cortex were next determined by Robert P.566

Desimone and his colleagues by presenting two stimuli, both falling in the receptive field of one cell. The experimenters found that they could turn a neuron on or off depending on whether they required the monkey to attend to one of the stimuli. The stimulus remained the same between trials; only the monkey's attention shifted.

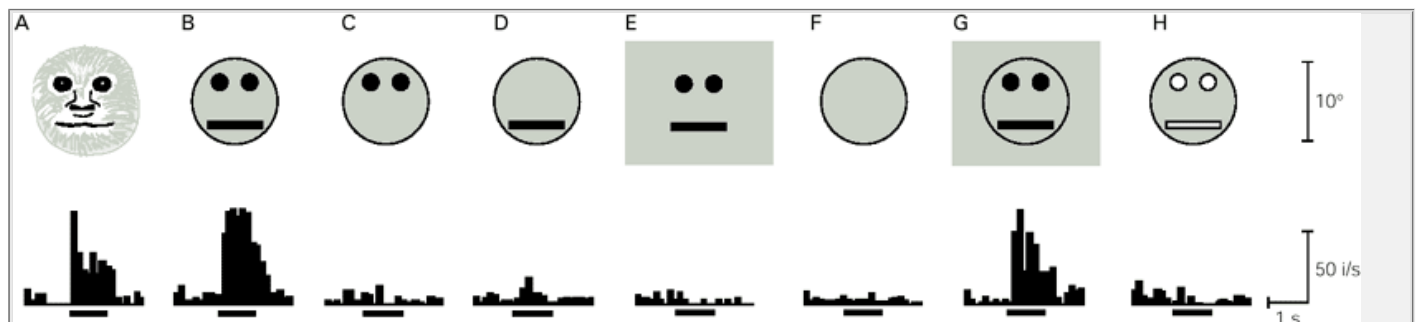


Figure 28-18 Response of a neuron in the inferior temporal cortex to complex stimuli. The cell responds strongly to the face of a toy monkey (A). The critical features producing the response are revealed in a configuration of two black spots and one horizontal black bar arranged on a gray disk (B). The bar, spots, and circular outline together were essential, as can be seen by the cell's responses to images missing one or more of these features (C, D, E, F). The contrast between the inside and outside of the circular contour was not critical (G). However, the spots and bar had to be darker than the background within the outline (H). (i = spikes.) (Modified from Kobatake and Tanaka 1994.)

Since attention is the selection of one stimulus from among many, it would be reasonable to expect that the effect of attention on cell responsiveness would increase with the number of stimuli presented. In one experiment a monkey was required to focus attention on one stimulus in a group of six to eight identical stimuli. The responses of one-third of the neurons in V4 were altered when the monkey's attention shifted to one stimulus. Activity in most of these same neurons was not altered as much when the monkey had to choose from only two identical stimuli. Furthermore, increasing the number of stimuli also enhanced the responses of neurons in earlier stages of the visual pathways, in V2 and V1. As the demands for selection among visual targets increases, so does the relative effect of attention.

Changes in cellular activity also occur when the focus of attention is a specific object rather than a location. In one set of experiments a monkey was cued to select an object, or the color or shape of an object, and then required to select a similar object from among a set of objects presented either simultaneously or in series. Remarkably, presentation of the matching object can have a greater effect on a neuron's response than the sample stimulus that is present. In one of these experiments the cells in V4 responded more vigorously when the color of the matching object was the same as the cue (Figure 28-19). During the search for matching stimuli the activity of neurons in the ventral pathway and inferior temporal cortex is modified. In the dorsal pathway the activity of cells in area 7A, MST, and MT is also modified, particularly when multiple stimuli fall within the receptive field of a cell.

The Binding Problem in the Visual System

We have seen that information about motion, depth, form, and color is processed in many different visual areas and organized into at least two cortical pathways. How can such distributed processing lead to cohesive perceptions? When we see a red ball we combine into one perception the sensations of color (red), form (round), and solidity (ball). We can equally well combine red with a square box, a pot, or a shirt. The possible combination of elements is so great that the existence of an individual feature-detecting cell for each set of combinations is improbable.

Instead, as we have seen in this chapter, the evidence is strongly in favor of a constructive process by which complex visual images are built up at successively higher processing centers. Is there a "final common pathway" where all the elements of a complex percept are brought together? Or do the distributed afferent pathways interact in some continuous fashion to produce coherent percepts? There is as yet no satisfactory solution to the *binding problem*, the problem of how consciousness of an ongoing, coherent experience emerges from the information processing being conducted independently in different cortical areas.

As described in Chapter 25, Anne Treisman and Bela Julesz independently showed that the associative process by which multiple features of one object are

brought together in a coherent percept requires attention. They suggested that different properties are encoded in different feature maps during a preattentive stage of perception and that attention selects specific features in these different maps and ties them together (as illustrated in Figure 25-15).

Box 28-2 Parietal Cortex and Movement

The dorsal visual path extends to the posterior parietal cortex, which, based on clinical observations of patients with parietal damage, is known to be involved in the representation of the visual world and the planning of movement. Recent studies of neurons in the parietal cortex of monkeys have revealed several functionally distinct areas, which may account for the varied deficits following damage to the parietal cortex. The activity in most of these areas is related to the transition from sensory processing to the generation of movement.

Neurons in one of these subregions, the lateral intraparietal area, fire in connection with saccadic eye movements (Chapter 39). These neurons fire in response to a visual target, before a saccade to the target, and increase their activity just before the beginning of the saccade, indicating that the activity in these neurons is related both to the visual input and to the motor output of the brain. Between the sensory and motor events, continuing activity in these neurons depends on the condition under which the saccade is made, such as whether the saccade is made to a visual stimulus or the location of a remembered stimulus. Thus, although activity in these neurons is closely associated with the transition from sensory perception to motor movement, it is not exclusively related to one or the other.

These neurons also clearly receive information more complex than either pure sensory and pure motor information. Many neurons respond differently to the same visual stimulus, depending upon where in space the eyes and head are oriented, indicating that they receive input about eye position as well as the visual stimulus. Such neurons might be involved in shifting the frame of reference in which sensory information is processed (from eye to head to body; see Box 25-1) a shift that is necessary to control movements such as reaching. We therefore have strong evidence that parietal neurons are involved in putting visual information in the service of the motor systems and for compensating for the disruption to vision that results from such movement.

A related view of the effect of attention on the binding problem recently was advanced by John Reynolds and Robert Desimone. They based their interpretation on two observations already described in this chapter: neurons have larger and larger receptive fields at higher levels in the cortical visual pathways and attention to one of several stimuli falling in one of these large receptive fields increases the response to that stimulus. They assume that attention acts to increase the competitive advantage of the attended stimulus so that the effect of attention is to shrink the effective size of the field around the attended stimulus. Now instead of many stimuli with different characteristics such as color and form, only the one stimulus is functionally present in the receptive field. Because the effective receptive field now just includes that one stimulus, all the characteristics of the stimulus are effectively bound together.

Another approach to the binding problem has been emphasized by Charles Gray and Wolfgang Singer and Reinhold Eckhorn and their colleagues. They found that when an object activates a population of neurons in the visual cortex, the neurons tend to oscillate and fire in unison. They suggest that these oscillations are indicative of a synchrony among cells and that this synchrony of firing would bind together the activity of cells responding to different features of the same object. To combine the visual features (color, form, motion) of the same object, the synchrony between neurons would, according to this view, extend across neurons in different cortical areas.

Quite a different solution to the binding problem was proposed by Lance Optican, Barry Richmond, and their colleagues. They found that neurons extending from the lateral geniculate nucleus to the inferior temporal cortex convey more information if the temporal pattern of their discharge is considered. Instead of measuring the total number of spikes in a time period, they measured the distribution of the spikes in that time period and found that different stimulus features (eg, form, contrast, color) tended to be represented by different response patterns of the same cell. They propose that the pattern of discharge in each cell carries information about different features so that the problem of binding across cells, each representing a different feature, is eliminated. Cells in different areas would all convey some information about a number of stimulus features, but different cells would carry comparatively more or less about each feature.

Thus, while several solutions to the binding problem have been proposed, it still remains one of the central unsolved puzzles in our understanding of the neurobiological bases of perception.

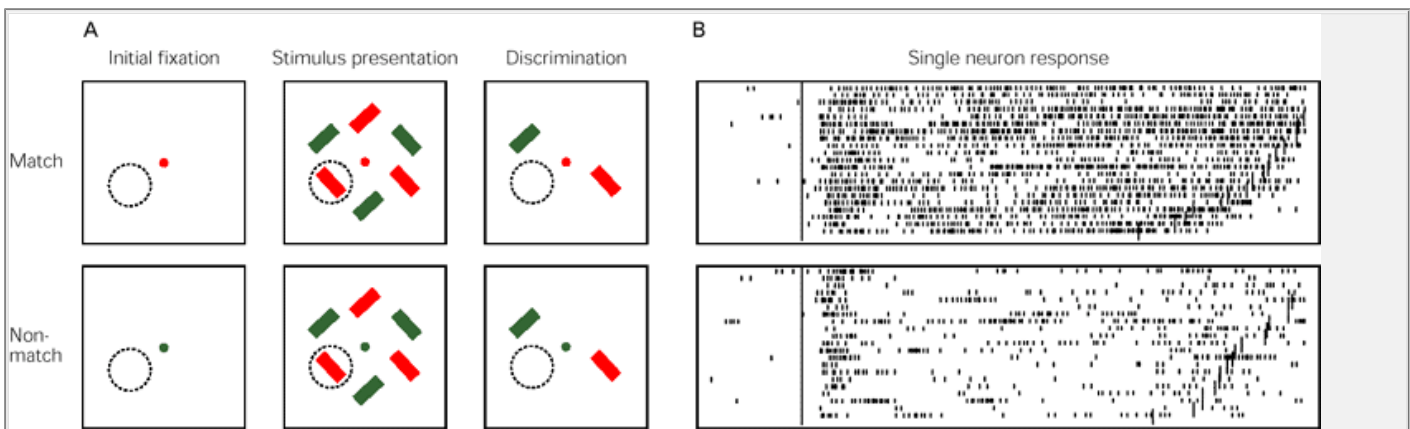


Figure 28-19 The response of V4 neurons to an effective visual stimulus is modified by selective attention.

A. A monkey was trained to shift its attention to one set of stimuli as opposed to another. At the start of each trial (**initial fixation**) the monkey was trained to look at a fixation point on a screen (the dot in the square). At this point in the experiment the receptive field of a V4 cell has been located (**dotted circle**). On any given trial the fixation point was either red (**upper row**) or green (**bottom row**). Then six other stimuli came on, one of which fell into the receptive field of the cell (**stimulus presentation**). The monkey knew from prior training that it would be required to discriminate only those stimuli that were the same color as the fixation point—the three red stimuli in the top row or the three green in the bottom row. The assumption in the experiment is that this requires the monkey to attend to the appropriate three stimuli. If one of those stimuli is in the receptive field of the cell, as in the match trials (top row), the monkey presumably is paying attention to that stimulus in the receptive field. If those stimuli with the same color as the fixation point lie outside the receptive field, as in the nonmatch trials (bottom row), the monkey presumably is attending to the stimuli outside the receptive field. The responses of the V4 neuron to these match and nonmatch trials were compared. Note that the stimulus falling on the receptive field of the cell is the same in the match and nonmatch trials were compared, only its significance for the monkey has changed. In the last phase of a trial (**discrimination**) only two stimuli remain on, and the monkey, in order to obtain a reward, must indicate whether the matched stimulus is tilted to the right or to the left.

B. Increased response to the same visual stimulus falling on the receptive field of a V4 cell during the match (upper record) as opposed to the nonmatch (lower record) trials. Each line represents a successive trial, and each dot indicates the discharge of the neuron. The vertical tick marks indicate the monkey's behavioral response. While the match and nonmatch trials are shown separately, they were interleaved during the experiment. (After [Motter 1994](#).)

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An Overall View

Much like the somatic sensory system the visual system consists of several parallel pathways not a single serial pathway. The M and P pathways pass from the retina, through the parvocellular and magnocellular layers of the lateral geniculate nucleus, to layer 4C of the primary visual cortex (V1), where they feed into parallel pathways extending through the cerebral cortex. A dorsal pathway extends from V1, through areas MT and MST, to the posterior parietal cortex. A ventral pathway extends from V1, through V4, to the inferior temporal cortex. The parietal pathway appears to be dominated by the M input, but the inferior temporal pathway depends upon both the P and the M input.

Several factors lead to the conclusion that these pathways serve different functions much as do the submodalities for somesthesia: The anatomical connections along these two pathways, differences in neuronal activity, the behavioral deficits occurring after damage to the terminal areas of the pathways in both humans and monkeys, and the activity detected in the human brain during tasks that should differentially activate the two pathways. One view is that the dorsal or posterior parietal pathway is concerned with determining where an object is, whereas the ventral or inferior temporal pathway is involved in recognizing what the object is. Another view is that the dorsal pathway leads to action, the ventral to perception. But all agree that the function of the two pathways is different.

We have concentrated on the neuronal mechanisms mediating motion and depth information in the dorsal posterior parietal pathway and on form perception in the ventral inferior temporal pathway. Both pathways represent hierarchies for visual processing that lead to greater abstraction at successive levels. Neurons in MT respond to the motion of a patterned stimulus, whereas cells in V1 respond only to motion of the elements of a pattern. Neurons in inferior temporal cortex respond to a given shape at any position in large areas of the visual

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field, whereas simple cells in V1 respond only when an edge is positioned at one location in the field. In addition, cellular responses along the pathways tend to become increasingly dependent on the stimulus characteristic selected for attention. The effect of the remembered object in a visual search can have more effect on the response of neurons in V4 and the inferior temporal cortex than the stimulus that is present.

While we have considered separately the visual processing for motion, depth, and form, these parallel pathways may not be mutually exclusive pathways. Some processing combines the activity of the pathways. For example, form can be seen when the only cue is the coherent motion of components of the scene (which is regarded as the purview of the parietal pathway). Likewise, some MT cells respond to the motion of an edge defined only by color (a property that should be conveyed by the inferior temporal pathway). Thus, at both a perceptual and a physiological level, cross talk between the posterior parietal and inferior temporal pathways must occur as is also indicated by the anatomical evidence for cross connections.

We know the outline of the steps the brain takes in constructing complex visual images from the pattern of light and dark falling on the retina—the early processing along the M and P pathways and the later, more abstract processing in the dorsal posterior parietal and ventral inferior temporal pathways. But these steps remain only an outline. Many cortical areas must still be explored, and critical details of visual processing are only beginning to be understood.

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