PRINCIPLES OF NEURAL SCIENCE

Fourth Edition

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Central Visual Pathways

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.

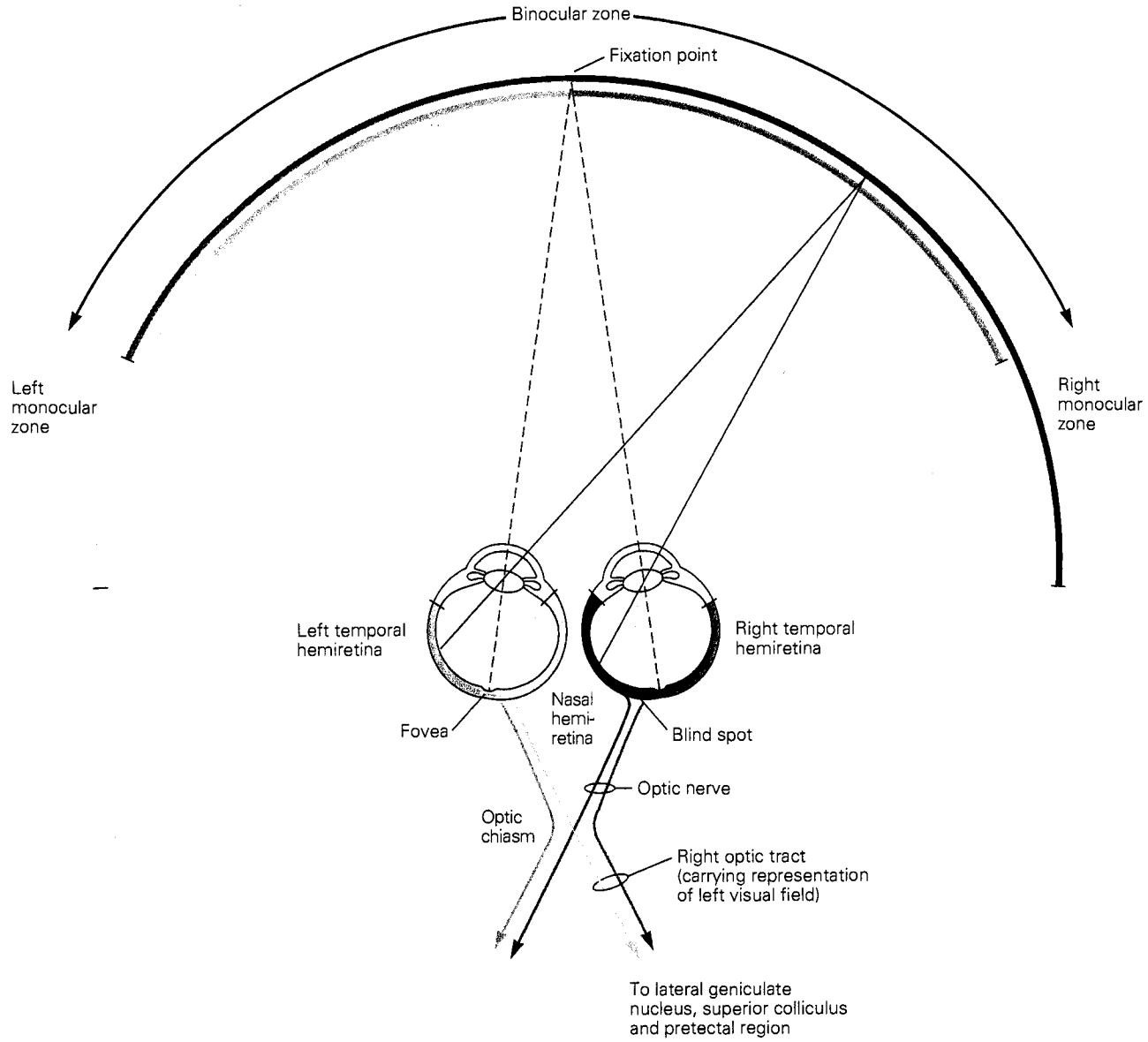


Figure 27-1 The visual field has both binocular and monocular zones. Light from the binocular zone strikes the retina in both eyes, whereas light from the monocular zone strikes the retina only in the eye on the same side. For example, light from a left monocular zone (temporal crescent) falls on only 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

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 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.

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.

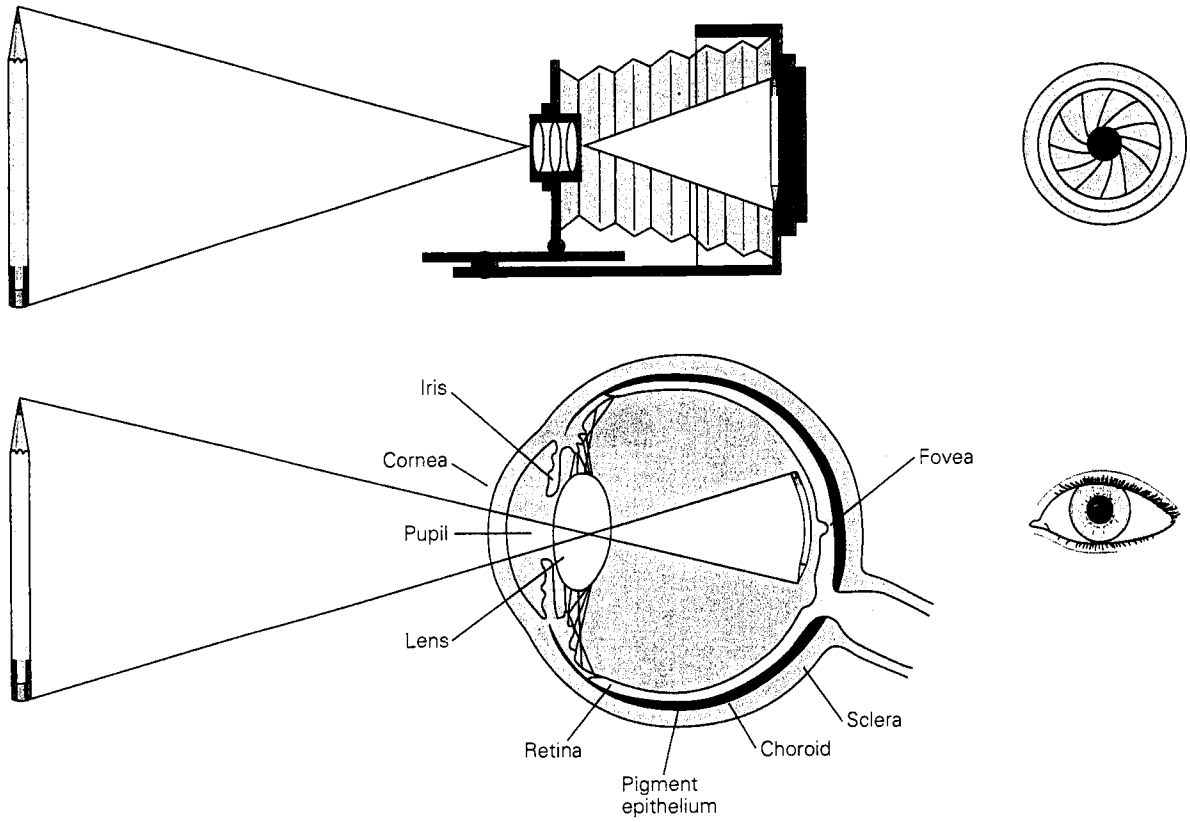


Figure 27-3 The lens of the eye projects an inverted image on the retina in the same way as a camera. (Adapted from Groves and Schlesinger 1979.)

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*

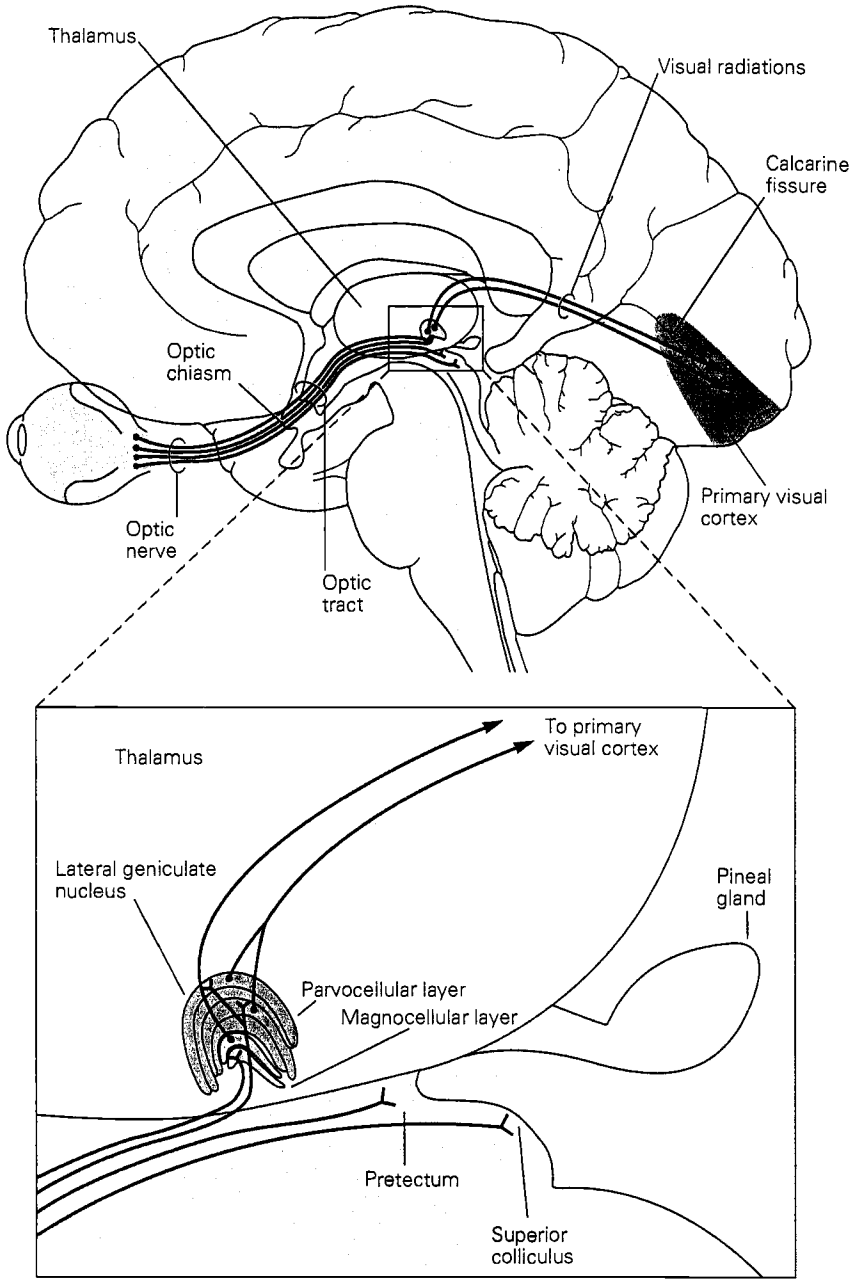


Figure 27-4 A simplified diagram of the projections from the retina to the visual areas of the thalamus (lateral geniculate nucleus) and midbrain (pretectum and superior colliculus). The retinal projection to the pretectal area is important for pupillary reflexes, and the projection to the superior colliculus 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.

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.

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 supe-

rior 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.

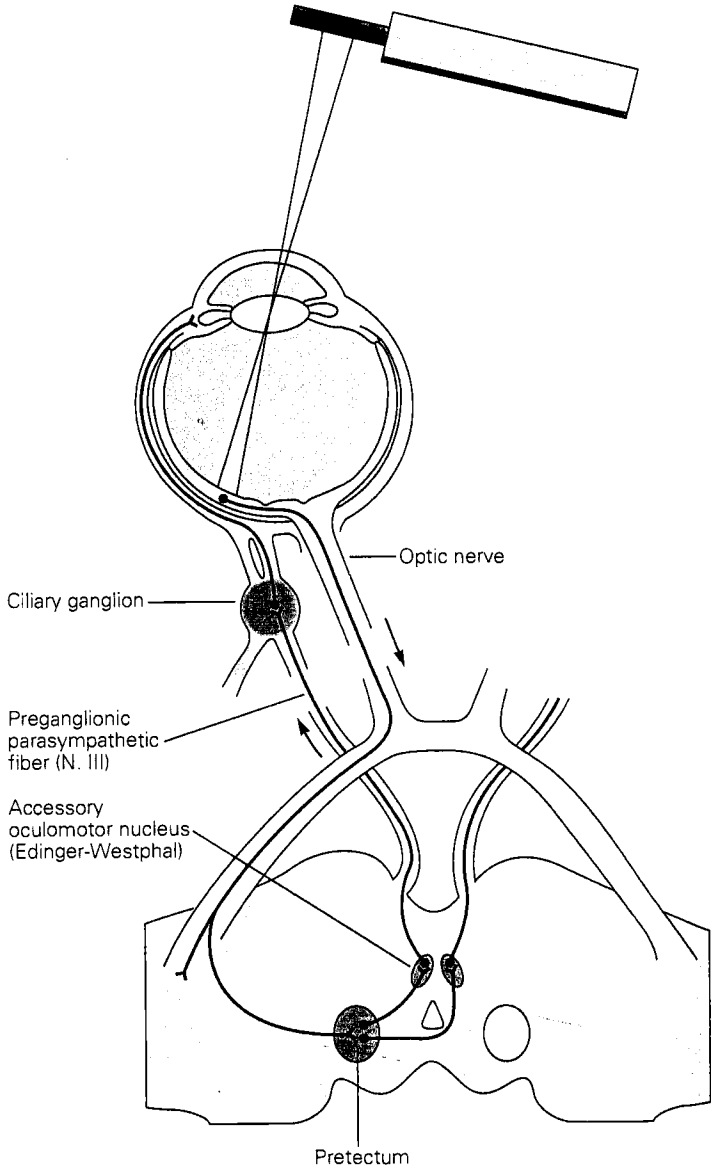


Figure 27-5 The reflex pathway mediating pupillary constriction. Light signals are relayed through the midbrain pretectum, to preganglionic parasympathetic neurons in the Edinger-Westphal nucleus, and out through the parasympathetic outflow of the oculomotor nerve to the ciliary ganglion. Postganglionic neurons then innervate the smooth muscle of the pupillary sphincter.

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

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.

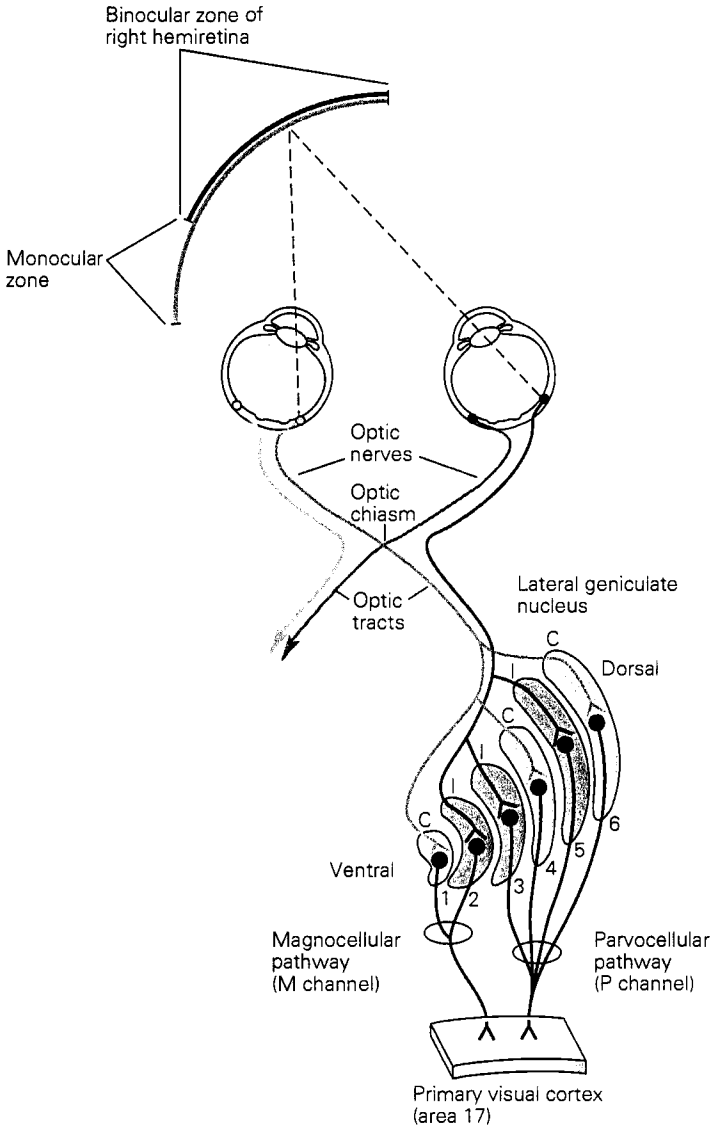


Figure 27-6 The lateral geniculate nucleus is the principal subcortical site for processing visual information. Inputs from the right hemiretina of each eye project to different layers of the right lateral geniculate nucleus to create a complete representation of the left visual hemifield. Similarly, 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 pro-

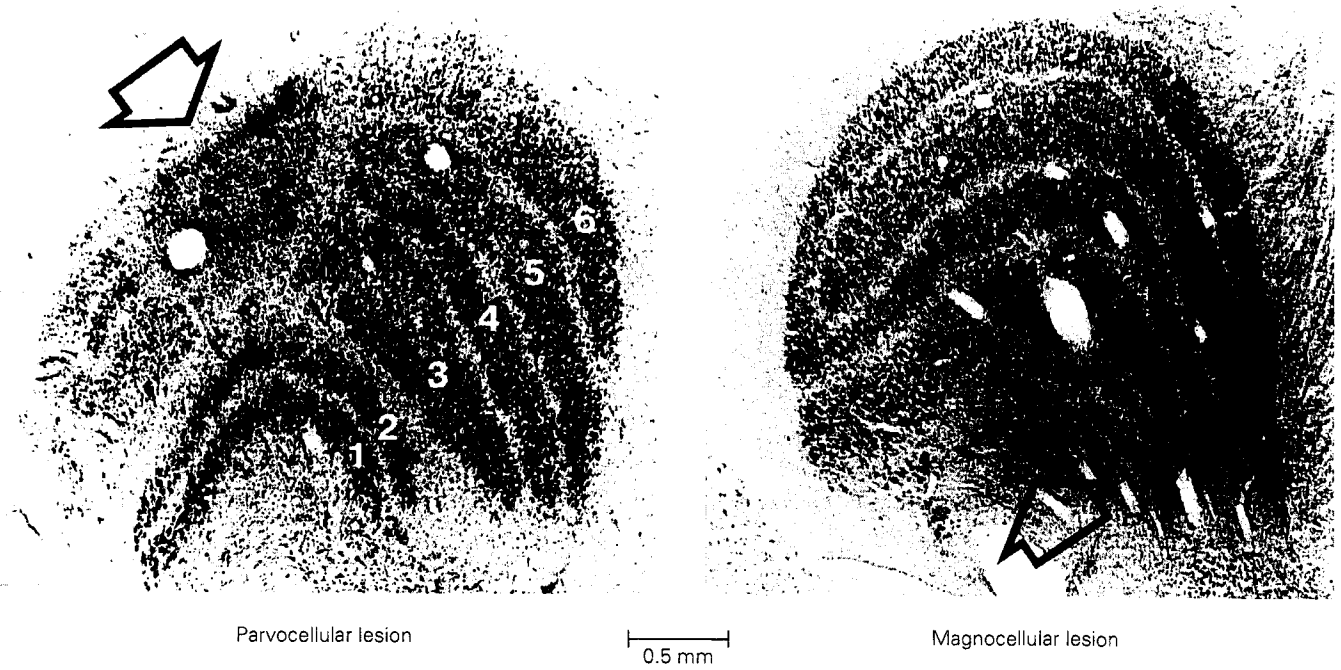


Figure 27-7 Samples of lesions (arrows) in the lateral geniculate nucleus of the monkey that selectively alter visual function. In the photograph on the left the geniculate layers are numbered. Lesions were made with an excitotoxin (ibotenic acid). Coronal sections were stained with cresyl violet. (From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

ject 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.

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

	Sensitivity	
Stimulus feature	**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).

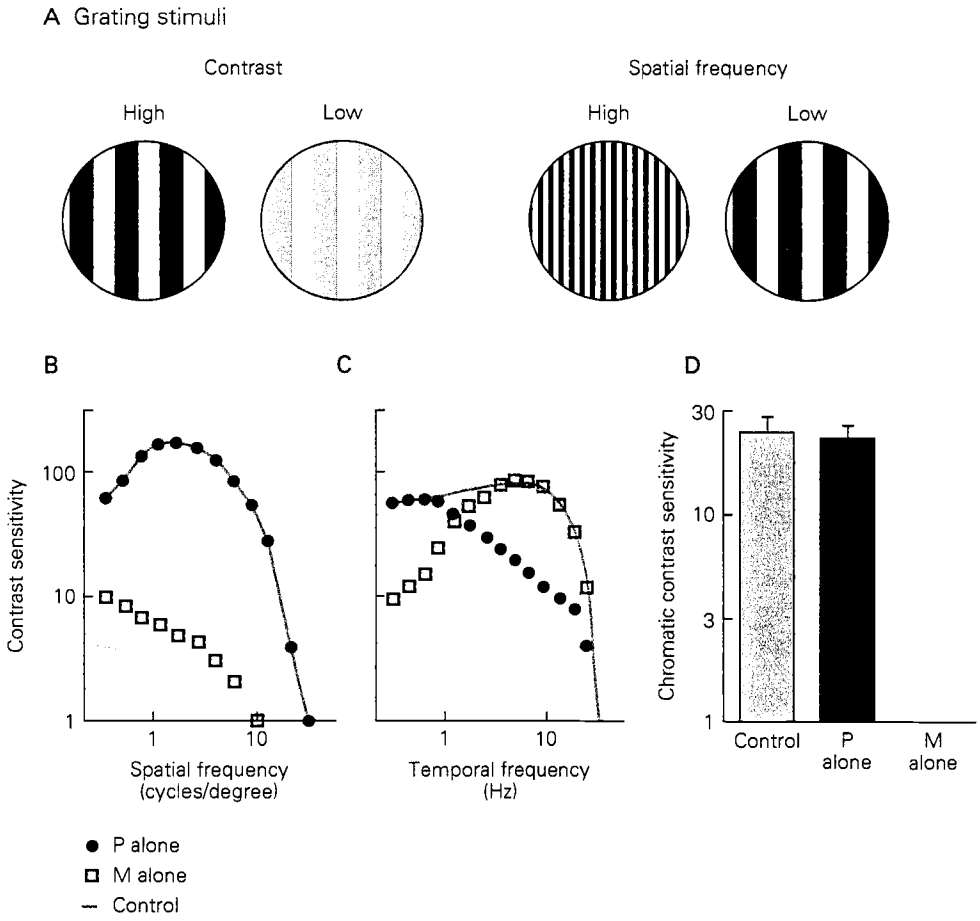


Figure 27-8 Visual losses after selective lesioning of the magnocellular and parvocellular layers of the lateral geniculate nucleus in monkeys. The monkeys were trained to look at a fixation spot on a TV monitor and then grating stimuli were presented at one location in the visual field. The location 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.)

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).

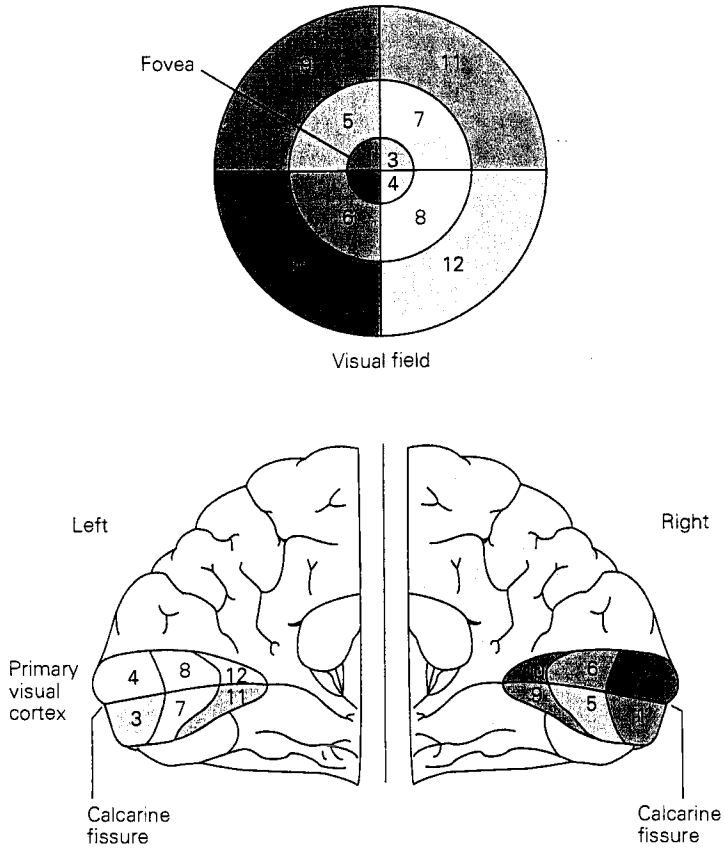


Figure 27-9 Each half of the visual field is represented in the contralateral primary visual cortex. In humans the primary visual cortex is located at the posterior pole of the cerebral hemisphere and lies almost exclusively on the medial surface. (In some individuals it is shifted so that part of it extends onto the lateral surface.) Areas in the primary visual cortex are devoted to specific parts of the visual field, as indicated by the corresponding numbers. The upper fields are mapped below the calcarine fissure, and the lower fields above it. The striking aspect of this map is that about half of the neural mass is devoted to representation of the fovea and the region just around it. This area has the greatest visual acuity.

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, 4Cα, and 4Cβ. 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 4Cα; the axons of most P cells terminate principally in sublamina 4Cβ (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

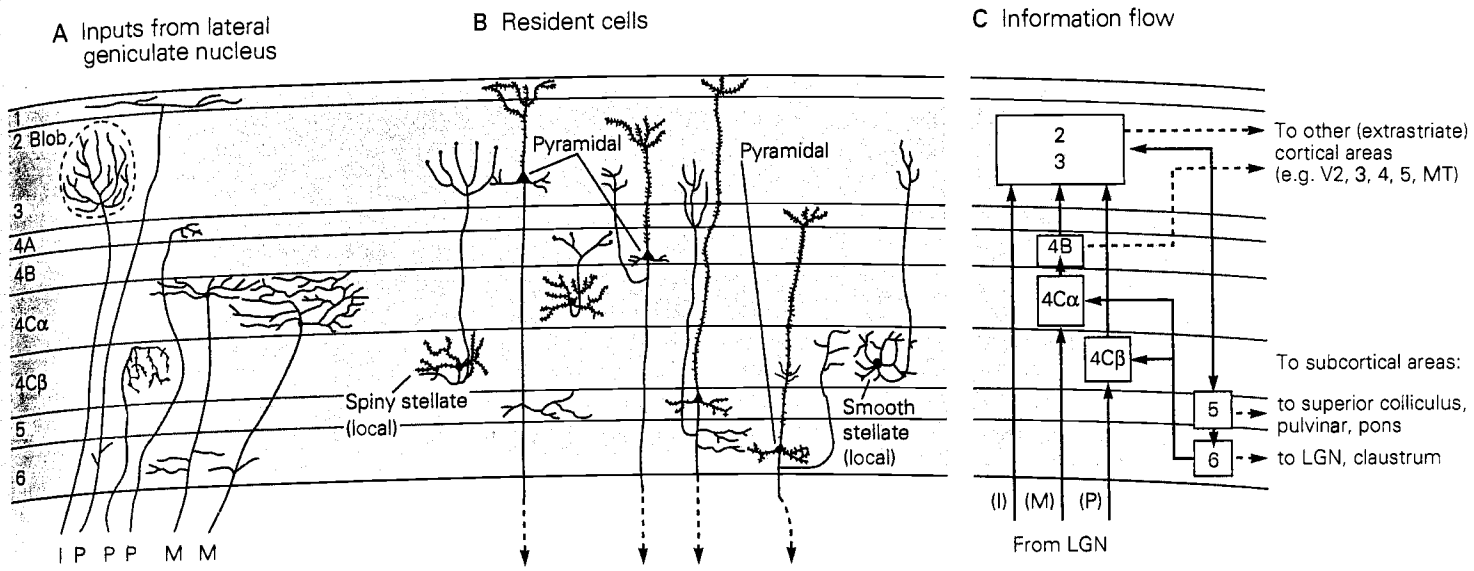


Figure 27-10 The primary visual cortex has distinct anatomical layers, each with characteristic synaptic connections. (Adapted from Lund 1988.)

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 4Cβ, with minor inputs to 4A and 1, while the axons of cells in the magnocellular layers (M) terminate primarily in layer 4Cα. 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.

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).

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.

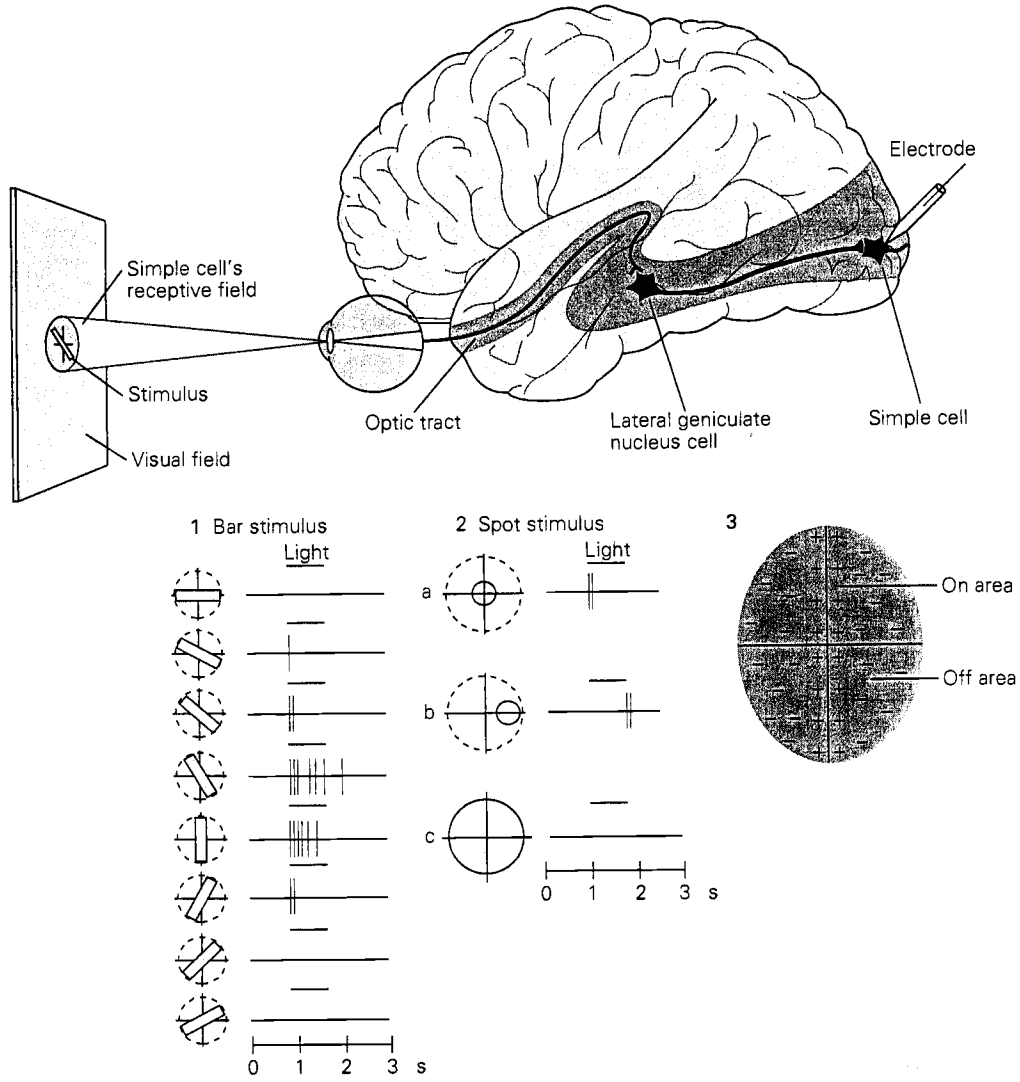


Figure 27-11 Receptive field of a simple cell in the primary visual cortex. The receptive field of a cell in the visual system is determined by recording activity in the cell while spots and bars of light are projected onto the visual field at an appropriate distance from the fovea. The records shown 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.

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

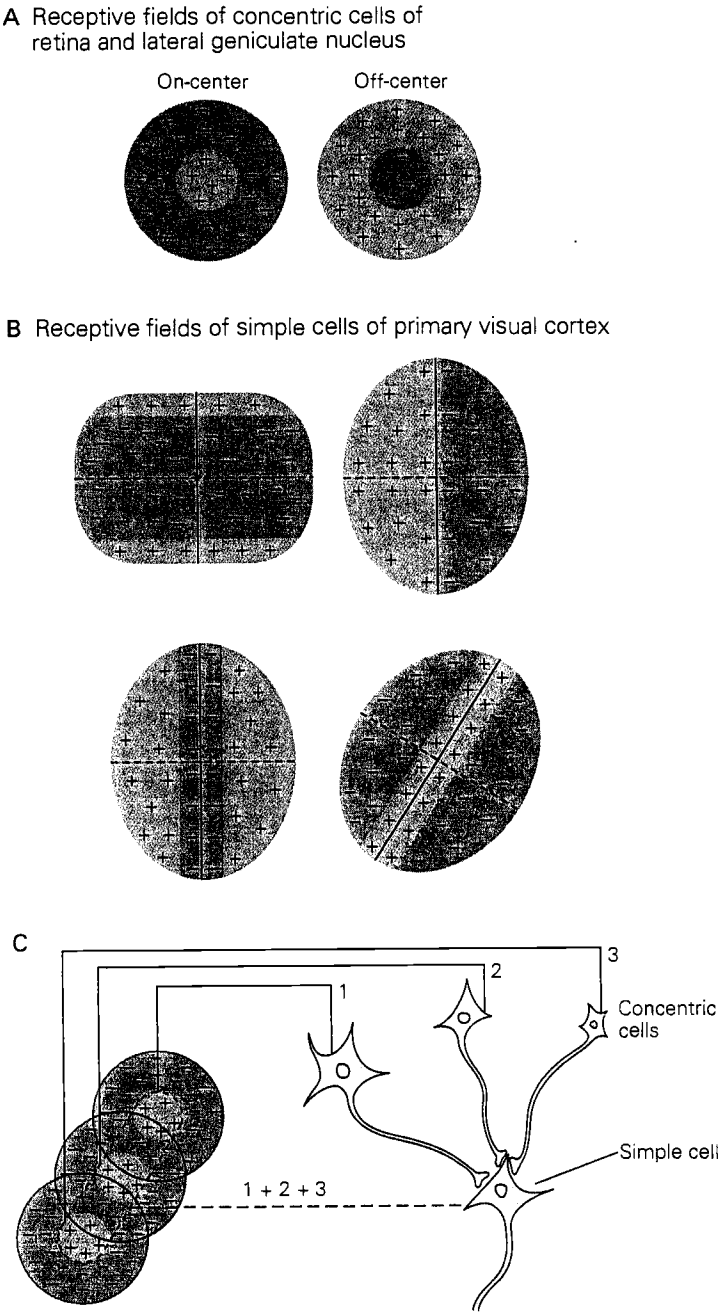


Figure 27-12 The receptive fields of simple cells in the primary visual cortex are different and more varied than those of the neurons in the retina and lateral geniculate nucleus.

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 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.

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

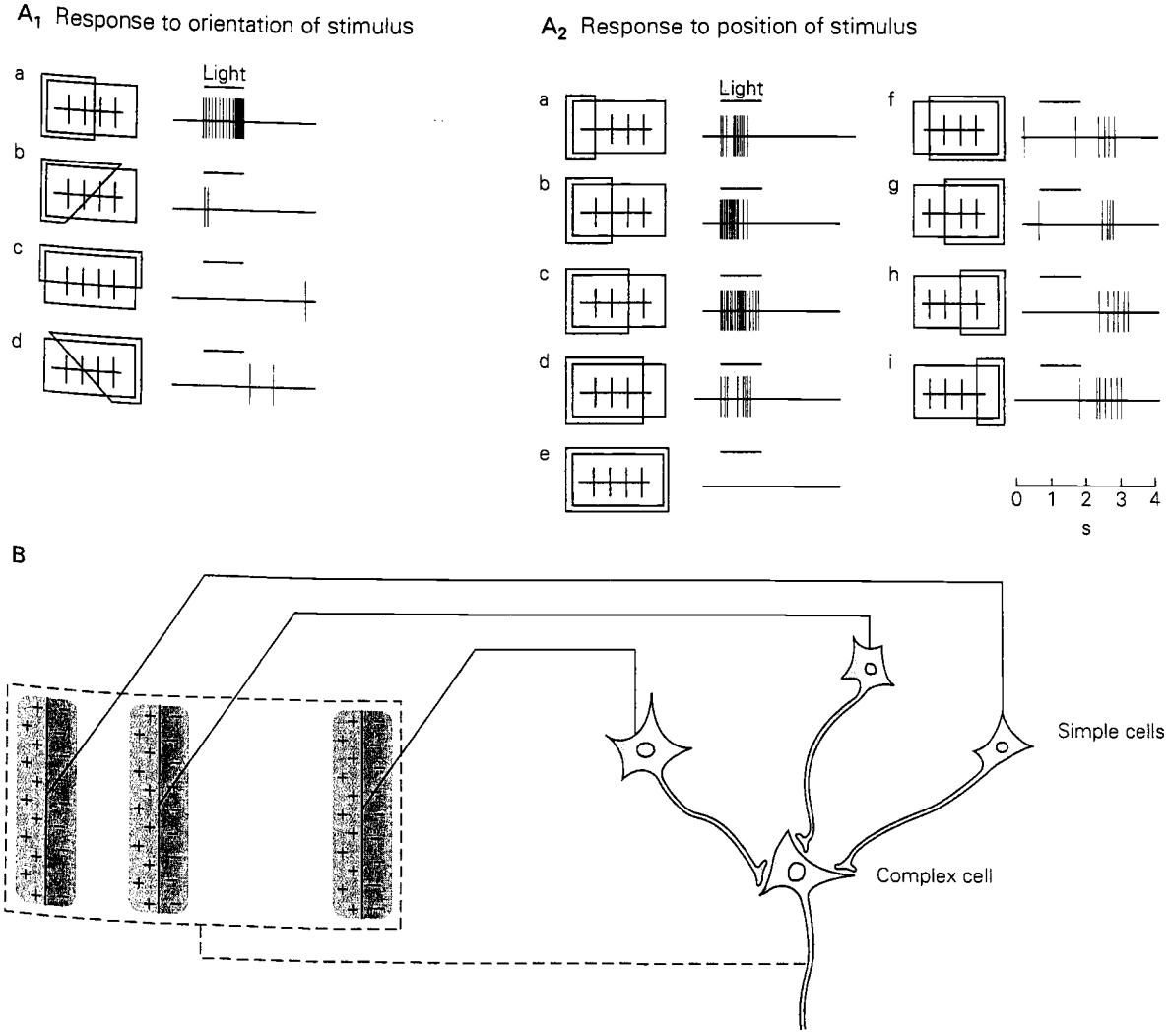


Figure 27-13 The receptive field of a complex cell in the primary visual cortex has no clearly excitatory or inhibitory zones. Orientation of the light stimulus is important, but position within the receptive field is not. (Adapted from Hubel and Wiesel 1962).

A. In this example the cell responds best to a vertical edge moving across the receptive field from left to right. This figure shows the patterns of action potentials fired by the cell in response to two types of variation in the stimulus: differences in orientation and differences in position. The line above each record indicates the period of illumination. **1.** Different orientations of the light stimulus produce different rates of firing in the cell. A vertical bar of light on the left of the receptive field produces a strong excitatory response (**a**). Orientations other than vertical are less effective (**b–d**). **2.** The position of the border of the light within the receptive field affects the type of response in the cell. If the edge of the light comes from any point on the right within the receptive field, the stimulus produces an excitatory response (**a–d**). If the edge comes from the left, the stimulus produces an inhibitory response (**f–i**). Illumination of the entire receptive field produces no response (**e**).

B. According to Hubel and Wiesel, the receptive fields of complex cells are determined by the pattern of inputs. Each complex cell receives convergent excitatory input from several simple cortical cells, each of which has a receptive field with the same organization: a central rectilinear excitation zone (+) and flanking inhibitory regions (−). In this way the receptive field of a complex cell is built up from the individual fields of the presynaptic cells.

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 trans-

formed 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

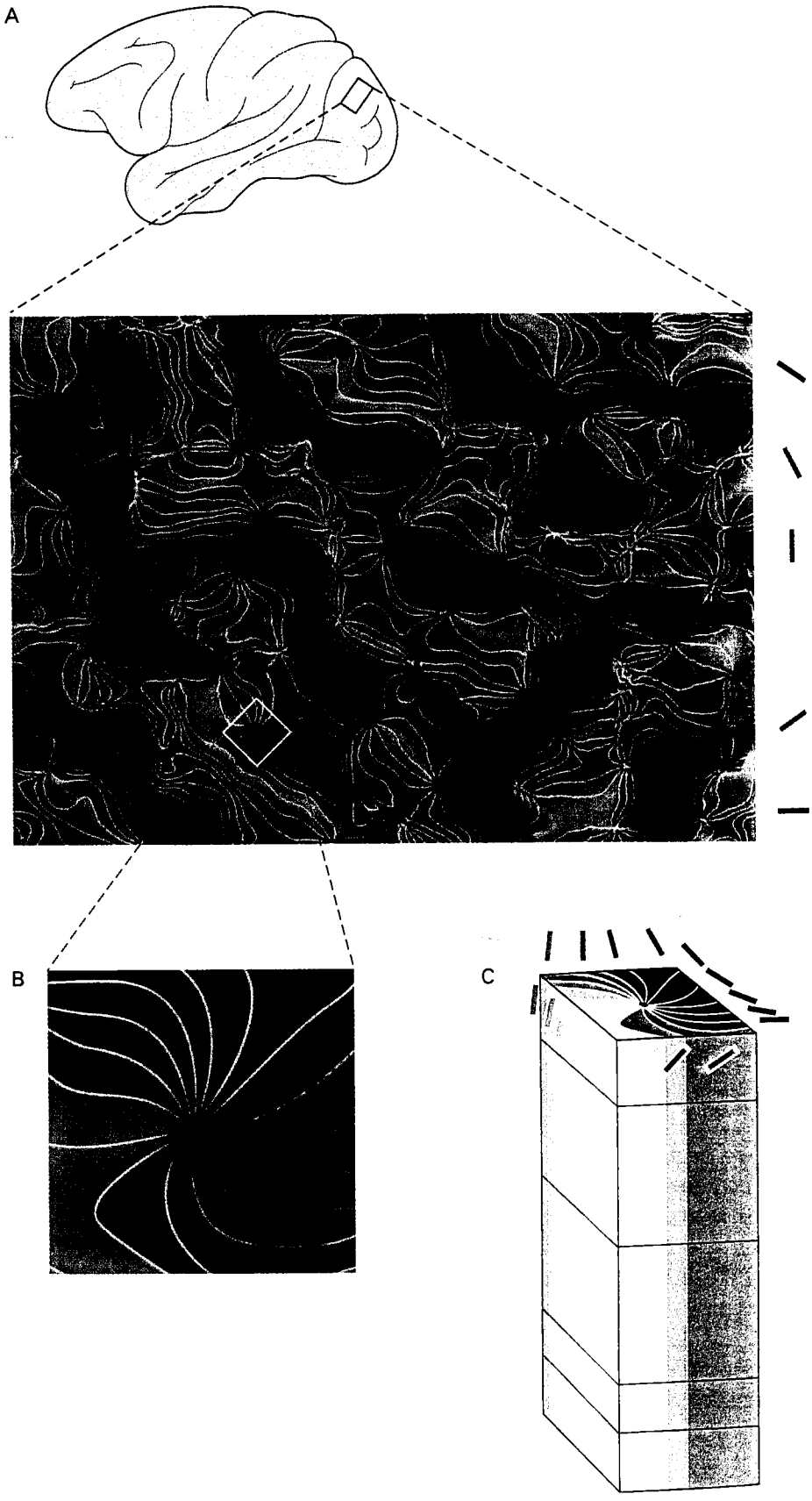


Figure 27-14 Orientation columns in the visual cortex of the monkey. (Courtesy of Gary Blasdel.)

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 ± 180°).

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

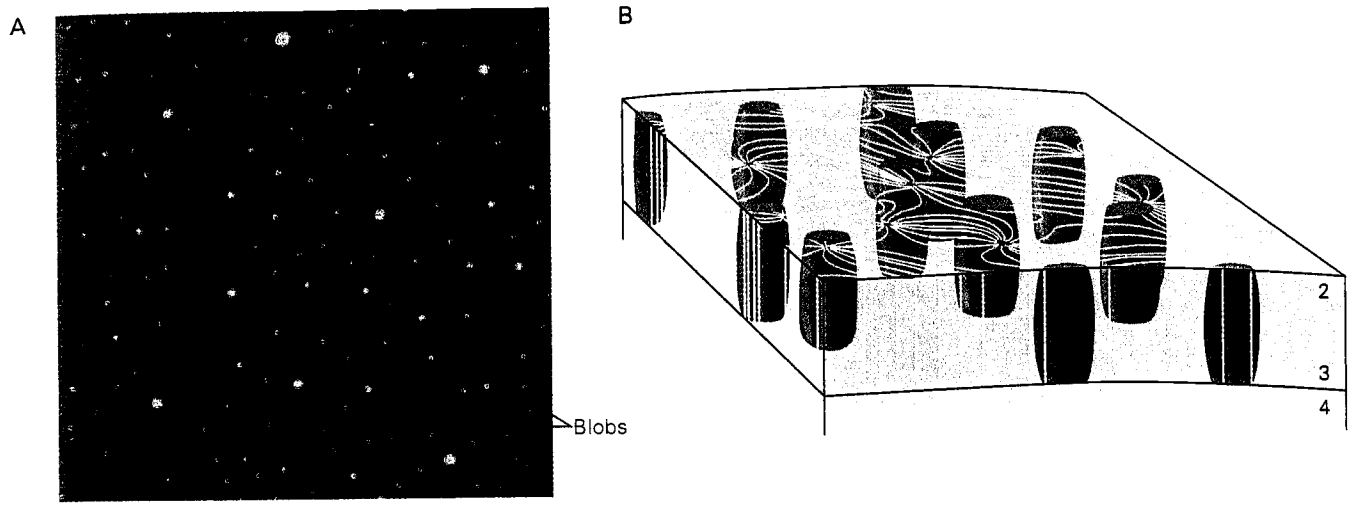


Figure 27-15 Organization of blobs in the visual cortex.

A. Blobs are visible as dark patches in this photograph of a single 40 μm 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 though these layers. The blobs interrupt the pattern of the orientation columns.

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.

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 mm^2. 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.

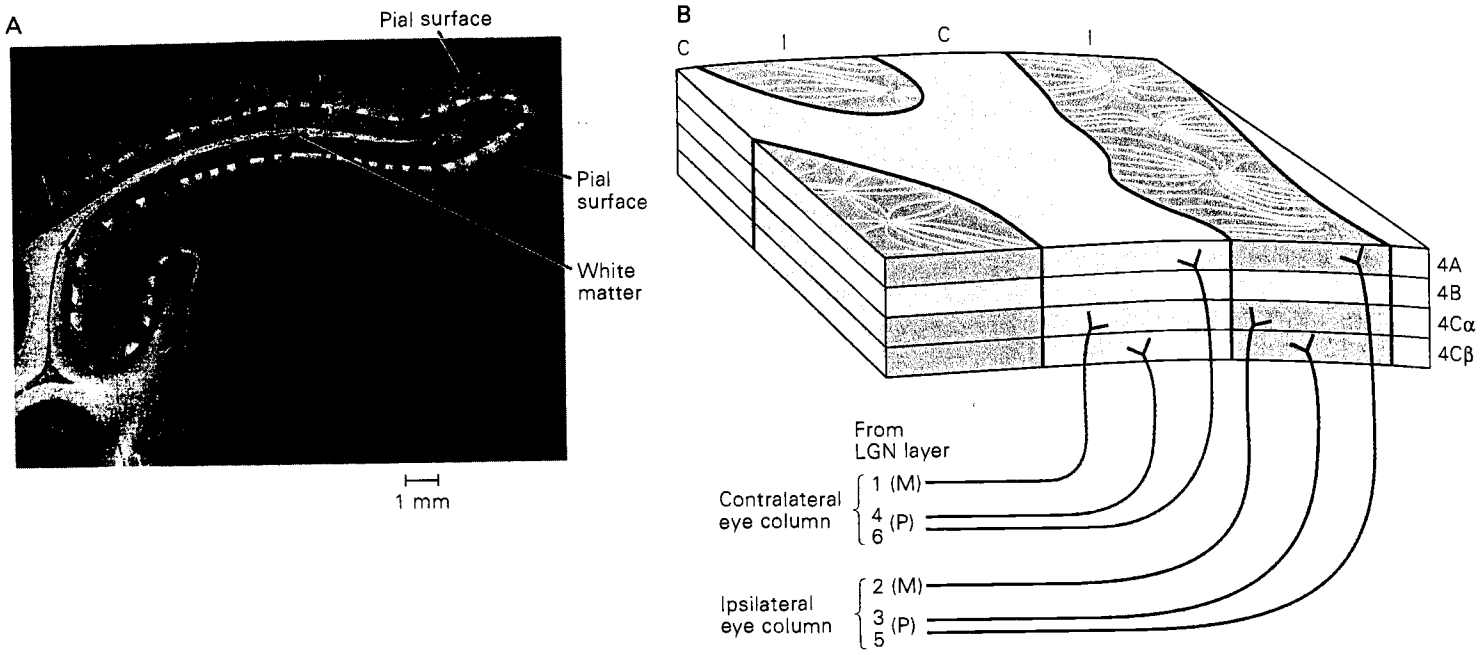


Figure 27-16 The ocular dominance columns.

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.

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

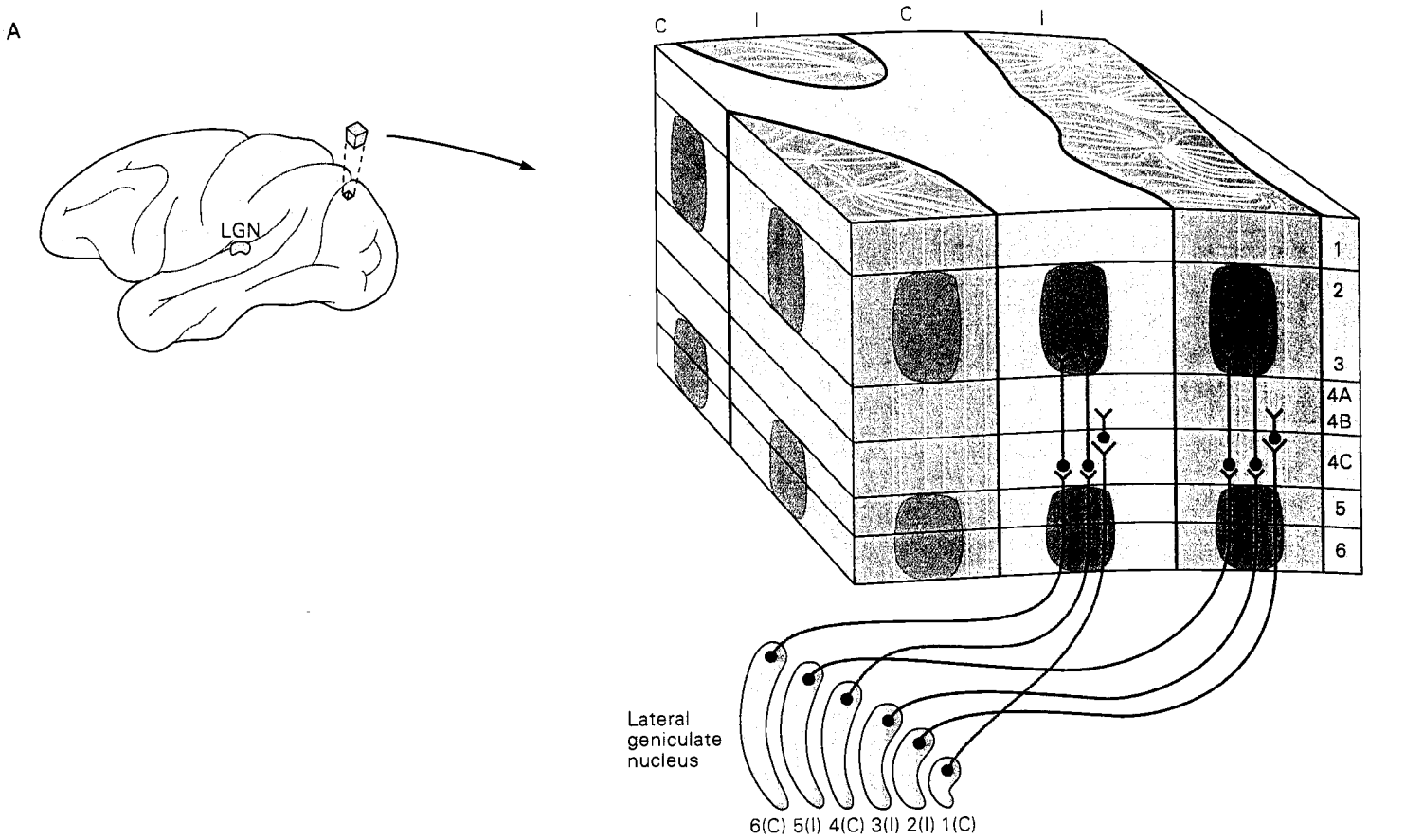
Columnar Units Are Linked by Horizontal Connections

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



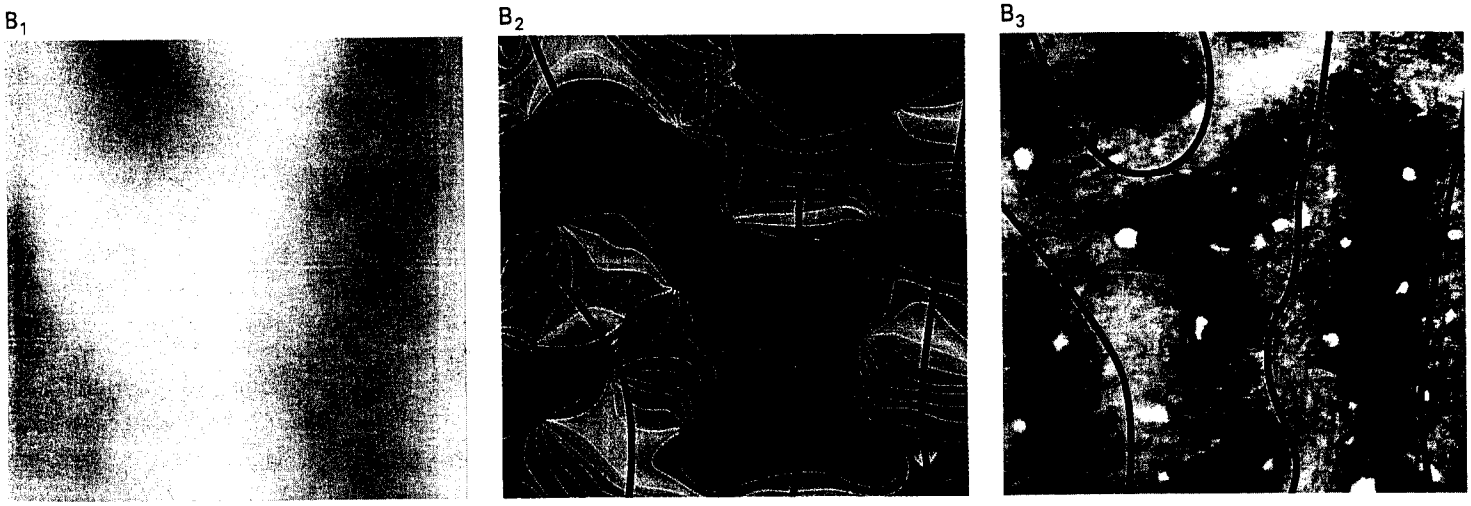


Figure 27-17 Organization of orientation columns, ocular dominance columns, and blobs in primary visual cortex.

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.

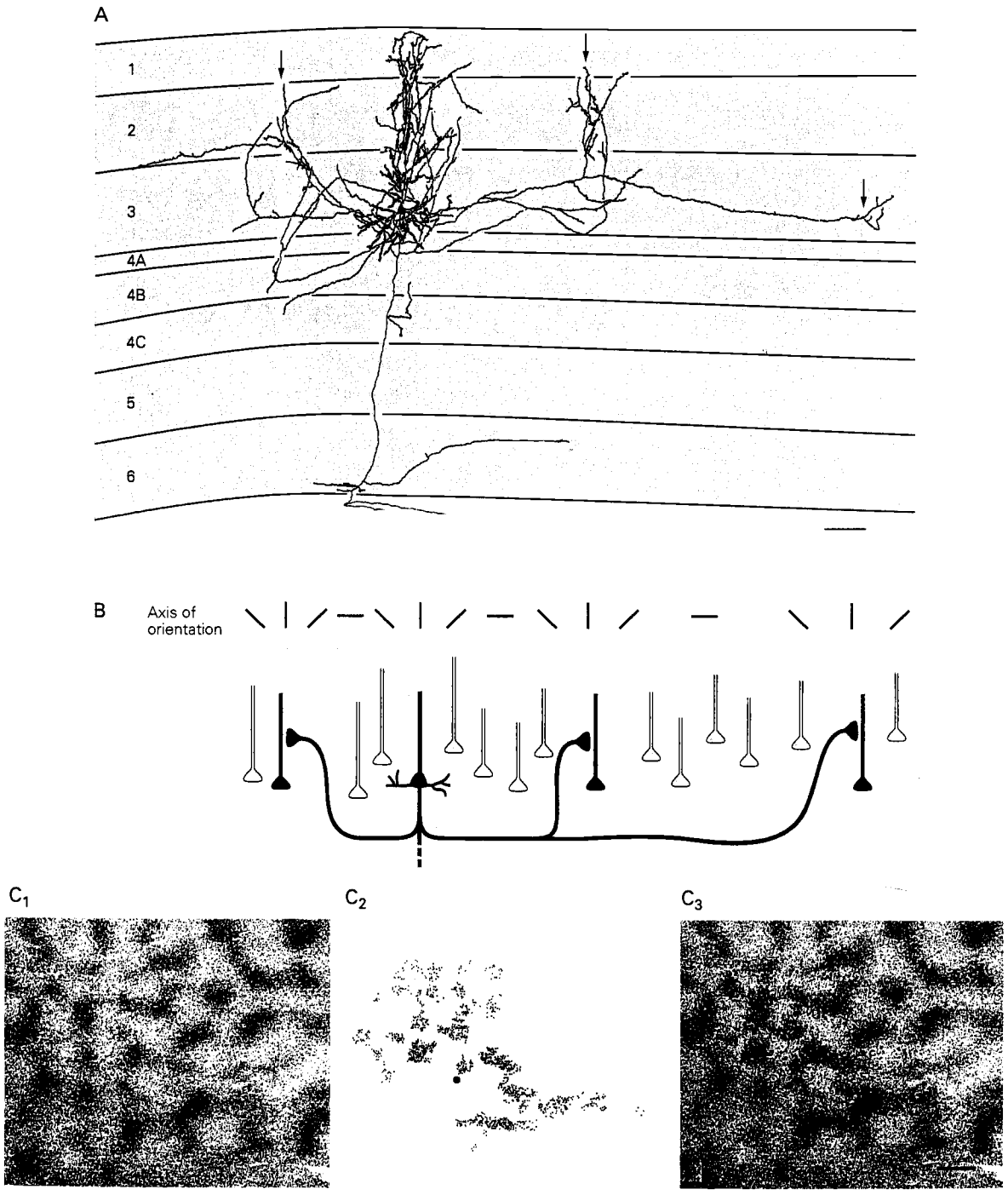


Figure 27-18 Columns of cells in the visual cortex with similar function are linked through horizontal connections.

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.)

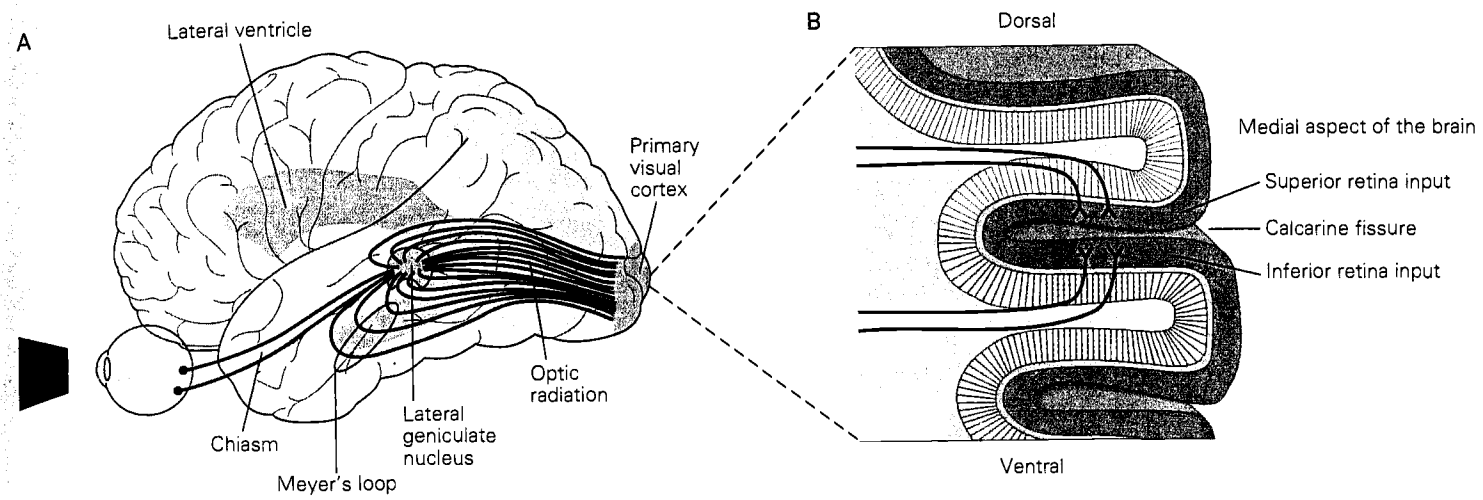


Figure 27-19 Projection of input from the retina to the visual cortex.

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.

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.

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 psychophysical 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

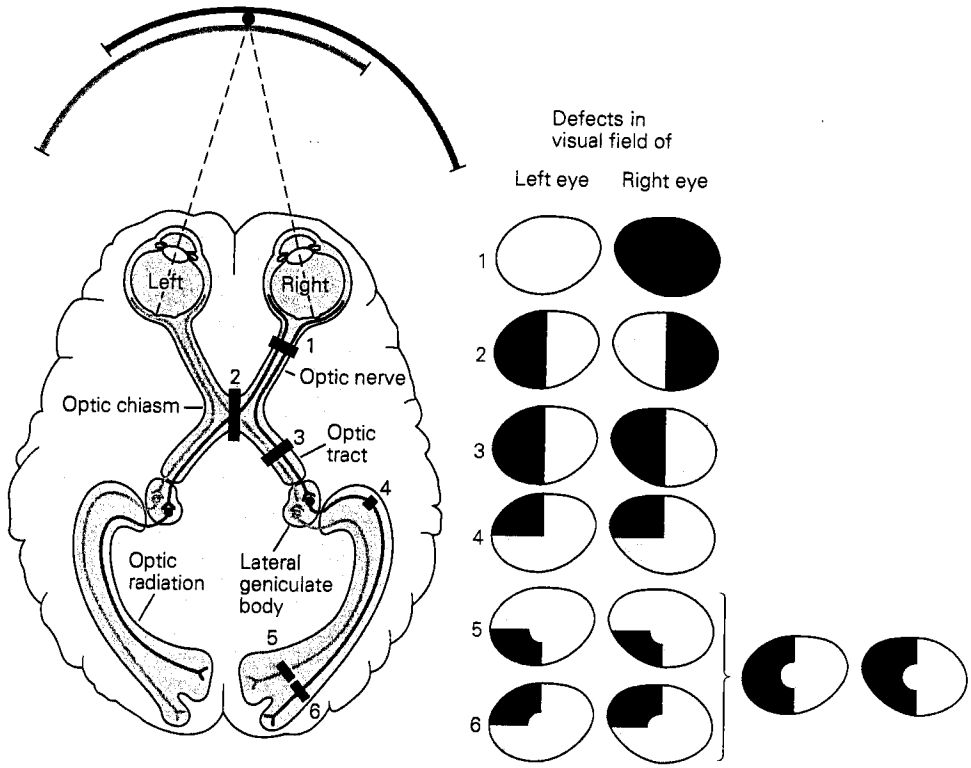


Figure 27-20 Deficits in the visual field produced by lesions at various points in the visual pathway. The level of a lesion can be determined by the specific deficit in the visual field. In the diagram of the cortex the numbers along the visual pathway indicate the sites of lesions. The deficits that 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.

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.

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). 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 *quadrantic 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 (4Cα and 4Cβ). 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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