Chapter 11



Central Visual Pathways

Overview

Information supplied by the retina initiates interactions between multiple subdivisions of the brain that eventually lead to conscious perception of the visual scene, at the same time stimulating more conventional reflexes such as adjusting the size of the pupil, directing the eyes to targets of interest, and regulating homeostatic behaviors that are tied to the day/night cycle. The pathways and structures that mediate this broad range of functions are necessarily diverse. Of these, the primary visual pathway from the retina to the dorsal lateral geniculate nucleus in the thalamus and on to the primary visual cortex is the most important and certainly the most thoroughly studied component of the visual system. Different classes of neurons within this pathway encode the varieties of visual information-luminance, spectral differences, orientation, and motion—that we ultimately see. The parallel processing of different categories of visual information continues in cortical pathways that extend beyond primary visual cortex, supplying a variety of visual areas in the occipital, parietal, and temporal lobes. Visual areas in the temporal lobe are primarily involved in object recognition, whereas those in the parietal lobe are concerned with motion. Normal vision depends on the integration of information in all these cortical areas. The processes underlying visual perception are not understood and remain one of the central challenges of modern neuroscience.

Central Projections of Retinal Ganglion Cells

Ganglion cell axons exit the retina through a circular region in its nasal part called the **optic disk** (or optic papilla), where they bundle together to form the **optic nerve**. This region of the retina contains no photoreceptors and, because it is insensitive to light, produces the perceptual phenomenon known as the **blind spot** (Box A). The optic disk is easily identified as a whitish circular area when the retina is examined with an ophthalmoscope; it also is recognized as the site from which the ophthalmic artery and veins enter (or leave) the eye (Figure 11.1). In addition to being a conspicuous retinal landmark, the appearance of the optic disk is a useful gauge of intracranial pressure. The subarachnoid space surrounding the optic nerve is continuous with that of the brain; as a result, increases in intracranial pressure—a sign of serious neurological problems such as a space-occupying lesion—can be detected as *papilledema*, a swelling of the optic disk.

Axons in the optic nerve run a straight course to the **optic chiasm** at the base of the diencephalon. In humans, about 60% of these fibers cross in the chiasm, while the other 40% continue toward the thalamus and midbrain targets on the same side. Once past the chiasm, the ganglion cell axons on each

Figure 11.1 The retinal surface of the left eye, viewed with an ophthalmoscope. The optic disk is the region where the ganglion cell axons leave the retina to form the optic nerve; it is also characterized by the entrance and exit, respectively, of the ophthalmic arteries and veins that supply the retina. The macula lutea can be seen as a distinct area at the center of the optical axis (the optic disk lies nasally); the macula is the region of the retina that has the highest visual acuity. The fovea is a depression or pit about 1.5 mm in diameter that lies at the center of the macula (see Chapter 10).



side form the **optic tract**. Thus, the optic tract, unlike the optic nerve, contains fibers from *both* eyes. The partial crossing (or decussation) of ganglion cell axons at the optic chiasm allows information from corresponding points on the two retinas to be processed by approximately the same cortical site in each hemisphere, an important issue that is considered in the next section.

The ganglion cell axons in the optic tract reach a number of structures in the diencephalon and midbrain (Figure 11.2). The major target in the diencephalon is the **dorsal lateral geniculate nucleus** of the thalamus. Neurons in the lateral geniculate nucleus, like their counterparts in the thalamic relays of other sensory systems, send their axons to the cerebral cortex via the internal capsule. These axons pass through a portion of the internal capsule called the **optic radiation** and terminate in the **primary visual cortex**, or **striate cortex** (also referred to as **Brodmann's area 17** or **V1**), which lies largely along and within the calcarine fissure in the occipital lobe. The **retinogeniculostriate pathway**, or **primary visual pathway**, conveys information that is essential for most of what is thought of as seeing. Thus, damage anywhere along this route results in serious visual impairment.

A second major target of the ganglion cell axons is a collection of neurons that lies between the thalamus and the midbrain in a region known as the **pretectum**. Although small in size compared to the lateral geniculate nucleus, the pretectum is particularly important as the coordinating center for the **pupillary light reflex** (i.e., the reduction in the diameter of the pupil that occurs when sufficient light falls on the retina) (Figure 11.3). The initial component of the pupillary light reflex pathway is a bilateral projection from the retina to the pretectum. Pretectal neurons, in turn, project to the **Edinger-Westphal nucleus**, a small group of nerve cells that lies close to the nucleus of the oculomotor nerve (cranial nerve III) in the midbrain. The Edinger-Westphal nucleus contains the preganglionic parasympathetic neurons that send their axons via the oculomotor nerve to terminate on neurons in the ciliary



Figure 11.2 Central projections of retinal ganglion cells. Ganglion cell axons terminate in the lateral geniculate nucleus of the thalamus, the superior colliculus, the pretectum, and the hypothalamus. For clarity, only the crossing axons of the right eye are shown (view is looking up at the inferior surface of the brain).



ganglion (see Chapter 19). Neurons in the ciliary ganglion innervate the constrictor muscle in the iris, which decreases the diameter of the pupil when activated. Shining light in the eye thus leads to an increase in the activity of pretectal neurons, which stimulates the Edinger-Westphal neurons and the ciliary ganglion neurons they innervate, thus constricting the pupil.

In addition to its normal role in regulating the amount of light that enters the eye, the pupillary reflex provides an important diagnostic tool that allows the physician to test the integrity of the visual sensory apparatus, the motor outflow to the pupillary muscles, and the central pathways that medi**Figure 11.3** The circuitry responsible for the pupillary light reflex. This pathway includes bilateral projections from the retina to the pretectum and projections from the pretectum to the Edinger-Westphal nucleus. Neurons in the Edinger-Westphal nucleus terminate in the ciliary ganglion, and neurons in the ciliary ganglion innervate the pupillary constrictor muscles. Notice that the afferent axons activate both Edinger-Westphal nuclei via the neurons in the pretectum.



Box A The Blind Spot

It is logical to suppose that a visual field defect (called a scotoma) arising from damage to the retina or central visual pathways would be obvious to the individual suffering from such pathology. When the deficit involves a peripheral region of the visual field, however, a scotoma often goes unnoticed until a car accident or some other mishap all too dramatically reveals the sensory loss. In fact, all of us have a physiological scotoma of which we are quite unaware, the so-called "blind spot." The blind spot is the substantial gap in each monocular visual field that corresponds to the location of the optic disk, the receptor-free region of the retina where the optic nerve leaves the eye (see Figure 11.1).

To find the "blind spot" of the right eye, close the left eye and fixate on the X shown in the figure here, holding the book about 30–40 centimeters away. Now take a pencil in your right hand and, without breaking fixation, move the tip slowly toward the X from the right side of the page. At some point, the tip of the pencil (indeed the whole end of the pencil) will disappear; mark this point and continue to move the pencil to the left until it reappears; then make another mark. The borders of the blind spot along the vertical axis can be determined in the same way by moving the pencil up and down so that its path falls between the two horizontal marks. To prove that information from the region of visual space bounded by the marks is really not perceived, put a penny inside the demarcated area. When you fixate the X with both eyes and then close the left eye, the penny will disappear, a seemingly magical event that amazed the French royal court when it was first reported by the natural philosopher Edmé Mariotte in 1668.

How can we be unaware of such a large defect in the visual field (typically about $5^{\circ}-8^{\circ}$? The optic disk is located in the nasal retina of each eye. With both eyes open, information about the corresponding region of visual space is, of course, available from the temporal retina of the other eye. But this fact does not explain why the blind spot remains undetected with one eye closed. When the world is viewed monocularly, the visual system appears to "fill-in" the missing part of the scene based on the information supplied by the regions surrounding the optic disk. To observe this phenomenon, notice what happens when a pencil or some other object lies across the optic disk representation. Remarkably, the pencil looks complete! Although electrophysiological recordings have shown that neurons in the visual

cortex whose receptive fields lie in the optic disk representation can be activated by stimulating the regions that surround the optic disk of the contralateral eye, suggesting that "filling-in" the blind spot is based on cortical mechanisms that integrate information from different points in the visual field, the mechanism of this striking phenomenon is not clear. Herman von Helmholtz pointed out in the nineteenth century that it may just be that this part of the visual world is ignored, the pencil being completed across the blind spot because the rest of the scene simply "collapses" around it.

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ate the reflex. Under normal conditions, the pupils of both eyes respond identically, regardless of which eye is stimulated; that is, light in one eye produces constriction of both the stimulated eye (the direct response) and the unstimulated eye (the consensual response; see Figure 11.3). Comparing the response in the two eyes is often helpful in localizing a lesion. For example, a direct response in the left eye without a consensual response in the right eye suggests a problem with the visceral motor outflow to the right eye, possibly as a result of damage to the oculomotor nerve or Edinger-Westphal nucleus in the brainstem. Failure to elicit a response (either direct or indirect) to stimulation of the left eye if both eyes respond normally to stimulation of the right eye suggests damage to the sensory input from the left eye, possibly to the left retina or optic nerve.

There are several other important targets of retinal ganglion cell axons. One is the **suprachiasmatic nucleus** of the hypothalamus, a small group of neurons at the base of the diencephalon (see Box A in Chapter 20). The **retinohypothalamic pathway** is the route by which variation in light levels influences the broad spectrum of visceral functions that are entrained to the day/night cycle (see Chapters 20 and 27). Another target is the **superior colliculus**, a prominent structure visible on the dorsal surface of the midbrain (see Figure 1.14). The superior colliculus coordinates head and eye movements to visual (as well as other) targets; its functions are considered in Chapter 19.

The type of visual information required to perform the functions of these different retinal targets is quite different. Reading the text on this page, for example, requires a high-resolution sampling of the retinal image, whereas regulating circadian rhythms and adjusting the pupil accordingly require only a measure of overall changes in light levels, and little or no information about the features of the image. It should come as no surprise, then, that there is a diversity of ganglion cell types that provide information appropriate to the functions of these different targets.

Projections to the lateral geniculate nucleus (which are described in more detail later) arise from at least three broad classes of ganglion cells, whose tuning properties are appropriate for mediating the richness of visual perception (high acuity, color, motion). In contrast, projections to the hypothalamus and the pretectum arise from ganglion cells that lack these properties and are highly suited for detecting luminance flux. The retinal specializations responsible for constructing these distinct classes of retinal ganglion cells are only beginning to be identified; they include not only differences in ganglion cell synaptic connections, but in the locus of the phototransduction event itself. Unlike the majority of ganglion cells, which depend on rods and cones for their sensitivity to light, the ganglion cells that project to the hypothalamus and pretectum express their own light-sensitive photopigment (*melanopsin*) and are capable of modulating their response to changes in light levels in the absence of signals from rods and cones. The presence of light sensitivity within this class of ganglion cells presumably explains why normal circadian rhythms are maintained in animals that have completely lost form vision due to degeneration of rod and cone photoreceptors.

The Retinotopic Representation of the Visual Field

The spatial relationships among the ganglion cells in the retina are maintained in most of their central targets as orderly representations or "maps" of visual space. Most of these structures receive information from both eyes, requiring that these inputs be integrated to form a coherent map of individFigure 11.4 Projection of the visual fields onto the left and right retinas. (A) Projection of an image onto the surface of the retina. The passage of light rays through the pupil of the eve results in images that are inverted and left-right reversed on the retinal surface. (B) Retinal quadrants and their relation to the organization of monocular and binocular visual fields, as viewed from the back surface of the eyes. Vertical and horizontal lines drawn through the center of the fovea define retinal quadrants (bottom). Comparable lines drawn through the point of fixation define visual field quadrants (center). Color coding illustrates corresponding retinal and visual field quadrants. The overlap of the two monocular visual fields is shown at the top.



ual points in space. As a general rule, information from the left half of the visual world, whether it originates from the left or right eye, is represented in the right half of the brain, and vice versa.

Understanding the neural basis for the appropriate arrangement of inputs from the two eyes requires considering how images are projected onto the two retinas, and the central destination of the ganglion cells located in different parts of the retina. Each eye sees a part of visual space that defines its **visual field** (Figure 11.4A). For descriptive purposes, each retina and its corresponding visual field are divided into quadrants. In this scheme, the surface of the retina is subdivided by vertical and horizontal lines that intersect at the center of the fovea (Figure 11.4B). The vertical line divides the retina into **nasal** and **temporal divisions** and the horizontal line divides the retina into **superior** and **inferior divisions**. Corresponding vertical and horizontal lines in visual space (also called meridians) intersect at the **point of fixation** (the point in visual space that falls on the fovea) and define the quadrants of the visual field. The crossing of light rays diverging from different points on an object at the pupil causes the images of objects in the visual field to be inverted and left-right reversed on the retinal surface. As a result, objects in the temporal part of the visual field are seen by the nasal part of the retina, and objects in the superior part of the visual field are seen by the inferior part of the retina. (It may help in understanding Figure 11.4B to imagine that you are looking at the back surfaces of the retinas, with the corresponding visual fields projected onto them.)

With both eyes open, the two foveas are normally aligned on a single target in visual space, causing the visual fields of both eyes to overlap extensively (see Figure 11.4B and Figure 11.5). This **binocular field** of view consists of two symmetrical visual hemifields (left and right). The left binocular hemifield includes the nasal visual field of the right eye and the temporal visual field of the left eye; the right hemifield includes the temporal visual field of



Figure 11.5 Projection of the binocular field of view onto the two retinas and its relation to the crossing of fibers in the optic chiasm. Points in the binocular portion of the left visual field (B) fall on the nasal retina of the left eye and the temporal retina of the right eye. Points in the binocular portion of the right visual field (C) fall on the nasal retina of the right eye and the temporal retina of the left eye. Points that lie in the monocular portions of the left and right visual fields (A and D) fall on the left and right nasal retinas, respectively. The axons of ganglion cells in the nasal retina cross in the optic chiasm, whereas those from the temporal retina do not. As a result, information from the left visual field is carried in the right optic tract, and information from the right visual field is carried in the left optic tract.



Figure 11.6 Visuotopic organization of the striate cortex in the right occipital lobe, as seen in mid-sagittal view. (A) The primary visual cortex occupies a large part of the occipital lobe. The area of central vision (the fovea) is represented over a disproportionately large part of the caudal portion of the lobe, whereas peripheral vision is represented more anteriorly. The upper visual field is represented below the calcarine sulcus, the lower field above the calcarine sulcus. (B) Photomicrograph of a coronal section of the human striate cortex, showing the characteristic myelinated band, or stria, that gives this region of the cortex its name. The calcarine sulcus on the medial surface of the occipital lobe is indicated. (B courtesy of T. Andrews and D. Purves.)

the right eye and the nasal visual field of the left eye. The temporal visual fields are more extensive than the nasal visual fields, reflecting the size of the nasal and temporal retinas respectively. As a result, vision in the periphery of the field of view is strictly monocular, mediated by the most medial portion of the nasal retina. Most of the rest of the field of view can be seen by both eyes; i.e., individual points in visual space lie in the nasal visual field of one eye and the temporal visual field of the other. It is worth noting, however, that the shape of the face and nose impact the extent of this region of binocular vision. In particular, the inferior nasal visual fields are less extensive than the superior nasal fields, and consequently the binocular field of view is smaller in the lower visual field than in the upper (see Figure 11.4B).

Ganglion cells that lie in the nasal division of each retina give rise to axons that cross in the chiasm, while those that lie in the temporal retina give rise to axons that remain on the same side (see Figure 11.5). The boundary (or line of decussation) between contralaterally and ipsilaterally projecting ganglion cells runs through the center of the fovea and defines the border between the nasal and temporal hemiretinas. Images of objects in the left visual hemifield (such as point B in Figure 11.5) fall on the nasal retina of the left eye and the temporal retina of the right eye, and the axons from ganglion cells in these regions of the two retinas project through the right optic tract. Objects in the right visual hemifield (such as point C in Figure 11.5) fall on the nasal retina of the right eye and the temporal retina of the left eye; the axons from ganglion cells in these regions project through the left optic tract. As mentioned previously, objects in the monocular portions of the visual hemifields (points A and D in Figure 11.5) are seen only by the most peripheral nasal retina of each eye; the axons of ganglion cells in these regions (like the rest of the nasal retina) run in the contralateral optic tract. Thus, unlike the optic nerve, the optic tract contains the axons of ganglion cells that originate in both eyes and represent the contralateral field of view.

Optic tract axons terminate in an orderly fashion within their target structures thus generating well ordered maps of the contralateral hemifield. For the primary visual pathway, the map of the contralateral hemifield that is established in the lateral geniculate nucleus is maintained in the projections of the lateral geniculate nucleus to the striate cortex (Figure 11.6). Thus the



Right occipital lobe

fovea is represented in the posterior part of the striate cortex, whereas the more peripheral regions of the retina are represented in progressively more anterior parts of the striate cortex. The upper visual field is mapped below the calcarine sulcus, and the lower visual field above it. As in the somatic sensory system, the amount of cortical area devoted to each unit area of the sensory surface is not uniform, but reflects the density of receptors and sensory axons that supply the peripheral region. Like the representation of the hand region in the somatic sensory cortex, the representation of the macula is therefore disproportionately large, occupying most of the caudal pole of the occipital lobe.

Visual Field Deficits

A variety of retinal or more central pathologies that involve the primary visual pathway can cause visual field deficits that are limited to particular regions of visual space. Because the spatial relationships in the retinas are maintained in central visual structures, a careful analysis of the visual fields can often indicate the site of neurological damage. Relatively large visual field deficits are called **anopsias** and smaller ones are called **scotomas** (see Box A). The former term is combined with various prefixes to indicate the specific region of the visual field from which sight has been lost (Figures 11.7 and 11.8).

Damage to the retina or one of the optic nerves before it reaches the chiasm results in a loss of vision that is limited to the eye of origin. In contrast, damage in the region of the optic chiasm—or more centrally—results in specific types of deficits that involve the visual fields of both eyes (Figure 11.8). Damage to structures that are central to the optic chiasm, including the optic tract, lateral geniculate nucleus, optic radiation, and visual cortex, results in deficits that are limited to the contralateral visual hemifield. For example, interruption of the optic tract on the right results in a loss of sight in the left visual field (that is, blindness in the temporal visual field of the left eye and the nasal visual field of the right eye). Because such damage affects corresponding parts of the visual field in each eye, there is a complete loss of vision in the affected region of the binocular visual field, and the deficit is referred to as a **homonymous hemianopsia** (in this case, a left homonymous hemianopsia).



Figure 11.7 Course of the optic radiation to the striate cortex. Axons carrying information about the superior portion of the visual field sweep around the lateral horn of the ventricle in the temporal lobe (Meyer's loop) before reaching the occipital lobe. Those carrying information about the inferior portion of the visual field travel in the parietal lobe.

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Figure 11.8 Visual field deficits resulting from damage at different points along the primary visual pathway. The diagram on the left illustrates the basic organization of the primary visual pathway and indicates the location of various lesions. The right panels illustrate the visual field deficits associated with each lesion. (A) Loss of vision in right eye. (B) Bitemporal (heteronomous) hemianopsia. (C) Left homonymous hemianopsia. (E) Left homonymous hemianopsia with macular sparing.



In contrast, damage to the optic chiasm results in visual field deficits that involve noncorresponding parts of the visual field of each eye. For example, damage to the middle portion of the optic chiasm (which is often the result of pituitary tumors) can affect the fibers that are crossing from the nasal retina of each eye, leaving the uncrossed fibers from the temporal retinas intact. The resulting loss of vision is confined to the temporal visual field of each eye and is known as **bitemporal hemianopsia**. It is also called **heteronomous hemianopsia** to emphasize that the parts of the visual field that are lost in each eye do not overlap. Individuals with this condition are able to see in both left and right visual fields, provided both eyes are open. However, all information from the most peripheral parts of visual fields (which are seen only by the nasal retinas) is lost.

Left eve

Right eye

Damage to central visual structures is rarely complete. As a result, the deficits associated with damage to the chiasm, optic tract, optic radiation, or visual cortex are typically more limited than those shown in Figure 11.8. This is especially true for damage along the optic radiation, which fans out under the temporal and parietal lobes in its course from the lateral geniculate nucleus to the striate cortex. Some of the optic radiation axons run out into the temporal lobe on their route to the striate cortex, a branch called **Meyer's loop** (see Figure 11.7). Meyer's loop carries information from the superior portion of the contralateral visual field. More medial parts of the optic radiation, which pass under the cortex of the parietal lobe, carry information from the inferior portion of the contralateral visual field. Damage to parts of the temporal lobe with involvement of Meyer's loop can thus result in a superior

homonymous quadrantanopsia; damage to the optic radiation underlying the parietal cortex results in an inferior homonymous quadrantanopsia.

Injury to central visual structures can also lead to a phenomenon called *macular sparing*, i.e., the loss of vision throughout wide areas of the visual field, with the exception of foveal vision. Macular sparing is commonly found with damage to the cortex, but can be a feature of damage anywhere along the length of the visual pathway. Although several explanations for macular sparing have been offered, including overlap in the pattern of crossed and uncrossed ganglion cells supplying central vision, the basis for this selective preservation is not clear.

The Functional Organization of the Striate Cortex

Much in the same way that Stephen Kuffler explored the response properties of individual retinal ganglion cells (see Chapter 10), David Hubel and Torsten Wiesel used microelectrode recordings to examine the properties of neurons in more central visual structures.

The responses of neurons in the lateral geniculate nucleus were found to be remarkably similar to those in the retina, with a center-surround receptive field organization and selectivity for luminance increases or decreases. However, the small spots of light that were so effective at stimulating neurons in the retina and lateral geniculate nucleus were largely ineffective in visual cortex. Instead, most cortical neurons in cats and monkeys responded vigorously to light–dark bars or edges, and only if the bars were presented at a particular range of orientations within the cell's receptive field (Figure 11.9). The responses of cortical neurons are thus tuned to the orientation of edges, much like cone receptors are tuned to the wavelength of light; the peak in the tuning curve (the orientation to which a cell is most responsive) is referred to as the neuron's preferred orientation. By sampling the responses of a large number of single cells, Hubel and Weisel demonstrated that all edge orientations were roughly equally represented in visual cortex. As a





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result, a given orientation in a visual scene appears to be "encoded" in the activity of a distinct population of **orientation-selective neurons**.

Hubel and Wiesel also found that there are subtly different subtypes within a class of neurons that preferred the same orientation. For example, the receptive fields of some cortical cells, which they called **simple cells**, were composed of spatially separate "on" and "off" response zones, as if the "on" and "off" centers of lateral geniculate cells that supplied these neurons were arrayed in separate parallel bands. Other neurons, referred to as complex cells, exhibited mixed "on" and "off" responses throughout their receptive field, as if they received their inputs from a number of simple cells. Further analysis uncovered cortical neurons sensitive to the *length* of the bar of light that was moved across their receptive field, decreasing their rate of response when the bar exceeded a certain length. Still other cells responded selectively to the *direction* in which an edge moved across their receptive field. Although the mechanisms responsible for generating these selective responses are still not well understood, there is little doubt that the specificity of the receptive field properties of neurons in the striate cortex (and beyond) plays an important role in determining the basic attributes of visual scenes.

Another feature that distinguishes the responses of neurons in the striate cortex from those at earlier stages in the primary visual pathway is **binocularity**. Although the lateral geniculate nucleus receives inputs from both eyes, the axons terminate in separate layers, so that individual geniculate



neurons are monocular, driven by either the left or right eye but not by both (Figure 11.10; see also Figure 11.14). In some species, including most (but not all) primates, inputs from the left and right eyes remain segregated to some degree even beyond the geniculate because the axons of geniculate neurons terminate in alternating eye-specific columns within cortical layer IV—the so-called **ocular dominance columns** (see the next section). Beyond this point, the signals from the two eyes are combined at the cellular level. Thus, most cortical neurons have binocular receptive fields, and these fields are almost identical, having the same size, shape, preferred orientation, and roughly the same position in the visual field of each eye.

Bringing together the inputs from the two eyes at the level of the striate cortex provides a basis for stereopsis, the special sensation of depth that arises from viewing nearby objects with two eyes instead of one. Because the two eyes look at the world from slightly different angles, objects that lie in front of or behind the plane of fixation project to noncorresponding points on the two retinas. To convince yourself of this fact, hold your hand at arm's length and fixate on the tip of one finger. Maintain fixation on the finger as you hold a pencil in your other hand about half as far away. At this distance, the image of the pencil falls on noncorresponding points on the two retinas and will therefore be perceived as two separate pencils (a phenomenon called double vision, or diplopia). If the pencil is now moved toward the finger (the point of fixation), the two images of the pencil fuse and a single pencil is seen in front of the finger. Thus, for a small distance on either side of the plane of fixation, where the disparity between the two views of the world remains modest, a single image is perceived; the disparity between the two eye views of objects nearer or farther than the point of fixation is interpreted as depth (Figure 11.11).

Although the neurophysiological basis of stereopsis is not understood, some neurons in the striate cortex and in other visual cortical areas have receptive field properties that make them good candidates for extracting information about binocular disparity. Unlike many binocular cells whose monocular receptive fields sample the same region of visual space, these neurons have monocular fields that are slightly displaced (or perhaps differ in their internal organization) so that the cell is maximally activated by stimuli that fall on noncorresponding parts of the retinas. Some of these neurons (so-called **far cells**) discharge to disparities beyond the plane of fixation, while others (**near cells**) respond to disparities in front of the plane of fixation. The pattern of activity in these different classes of neurons seems likely to contribute to sensations of stereoscopic depth (Box B).

Interestingly, the preservation of the binocular responses of cortical neurons is contingent on the normal activity from the two eyes during early postnatal life. Anything that creates an imbalance in the activity of the two eyes—for example, the clouding of one lens or the abnormal alignment of the eyes during infancy (strabismus)—can permanently reduce the effective-ness of one eye in driving cortical neurons, and thus impair the ability to use binocular information as a cue for depth. Early detection and correction of visual problems is therefore essential for normal visual function in maturity (see Chapter 23).

The Columnar Organization of the Striate Cortex

The variety of response properties exhibited by cortical neurons raises the question of how neurons with different receptive fields are arranged within striate cortex. For the most part, the responses of neurons are qualitatively



Figure 11.11 Binocular disparities are generally thought to be the basis of stereopsis. When the eyes are fixated on point b, points that lie beyond the plane of fixation (point c) or in front of the point of fixation (point a) project to non-corresponding points on the two retinas. When these disparities are small, the images are fused and the disparity is interpreted by the brain as small differences in depth. When the disparities are greater, double vision occurs (although this normal phenomenon is generally unnoticed).

Box B Random Dot Stereograms and Related Amusements

An important advance in studies of stereopsis was made in 1959 when Bela Julesz, then working at the Bell Laboratories in Murray Hill, New Jersey, discovered an ingenious way of showing that stereoscopy depends on matching information seen by the two eyes without any prior recognition of what object(s) such matching might generate. Julesz, a Hungarian whose background was in engineering and physics, was working on the problem of how to "break" camouflage. He surmised that the brain's ability to fuse the slightly different views of the two eyes to bring out new information would be an aid in overcoming military camouflage. Julesz also realized that, if his hypothesis was correct, a hidden figure in a random pattern presented to the two eyes should emerge when a portion of the otherwise identical pattern was shifted horizontally in the view of one eye or the other. A horizontal shift in one direction would cause the hidden object to appear in front of the plane of the background, whereas a shift in the other direction would cause the hidden object to appear in back of the plane. Such a figure, called a random dot stereogram, and the method of its creation are shown in Figures A and B. The two images can be easily fused in a stereoscope (like the

Random dot stereograms and autostereograms. (A) to construct a random dot stereogram, a random dot pattern is created to be observed by one eye. The stimulus for the other eye is created by copying the first image, displacing a particular region horizontally, and then filling in the gap with a random sample of dots. (B) When the right and left images are viewed simultaneously but independently by the two eyes (by using a stereoscope or fusing the images by converging or diverging the eyes), the shifted region (a square) appears to be in a different plane from the other dots. (A after Wandell, 1995.) familiar Viewmaster[®] toy) but can also be fused simply by allowing the eyes to diverge. Most people find it easiest to do this by imagining that they are looking "through" the figure; after some seconds, during which the brain tries to make sense of what it is presented with, the two images merge and the hidden figure appears (in this case, a square that occupies the middle portion of the figure). The random dot stereogram has been widely used in stereoscopic research for about 40 years, although how such stimuli elicit depth remains very much a matter of dispute.

An impressive—and extraordinarily popular—derivative of the random dot stereogram is the autostereogram (Figure C). The possibility of autostereograms was first discerned by the nineteenthcentury British physicist David Brewster. While staring at a Victorian wallpaper with an iterated but offset pattern, he noticed that when the patterns were fused, he perceived two different planes. The plethora of autostereograms that can be seen today in posters, books, and newspapers are close cousins of the random dot stereogram in that computers are used to shift patterns of iterated



information with respect to each other. The result is that different planes emerge from what appears to be a meaningless array of visual information (or, depending on the taste of the creator, an apparently "normal" scene in which the iterated and displaced information is hidden). Some autostereograms are designed to reveal the hidden figure when the eyes diverge, and others when they converge. (Looking at a plane more distant than the plane of the surface causes divergence; looking at a plane in front of the picture causes the eyes to converge; see Figure 11.11.)

The elevation of the autostereogram to a popular art form should probably be attributed to Chris W. Tyler, a student of Julesz's and a visual psychophysicist, who was among the first to create commercial autostereograms. Numerous graphic artists—preeminently in Japan, where the popularity of the autostereogram has been enormous—have generated many of such images. As with the random dot stereogram, the task in viewing the autostereogram is not clear to the observer. Nonetheless, the hidden figure emerges, often after minutes of effort in which the brain automatically tries to make sense of the occult information.

(C)

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(C) An autostereogram. The hidden figure (three geometrical forms) emerges by diverging the eyes in this case. (C courtesy of Jun Oi.)

similar at any one point in primary visual cortex, but tend to shift smoothly across its surface. With respect to orientation, for example, all the neurons encountered in an electrode penetration perpendicular to the surface at a particular point will very likely have the same orientation preference, forming a "column" of cells with similar response properties. Adjacent columns, however, usually have slightly different orientation preferences; the sequence of orientation preferences encountered along a tangential electrode penetration gradually shifts as the electrode advances (Figure 11.12). Thus, orientation preference is mapped in the cortex, much like receptive field

Figure 11.12 Columnar organization of orientation selectivity in the monkey striate cortex. Vertical electrode penetrations encounter neurons with the same preferred orientations, whereas oblique penetrations show a systematic change in orientation across the cortical surface. The circles denote the lack of orientation-selective cells in layer IV.



location (Box C). Unlike the map of visual space, however, the map of orientation preference is iterated many times, such that the same orientation preference is repeated at approximately 1-mm intervals across the striate cortex. This iteration presumably ensures that there are neurons for each region of visual space that represent the full range of orientation values. The orderly progression of orientation preference (as well as other properties that are mapped in this systematic way) is accommodated within the orderly map of visual space by the fact that the mapping is relatively coarse. Each small region of visual space is represented by a set of neurons whose receptive fields cover the full range of orientation preferences, the set being distributed over several millimeters of the cortical surface

The columnar organization of the striate cortex is equally apparent in the binocular responses of cortical neurons. Although most neurons in the striate cortex respond to stimulation of both eyes, the relative strength of the inputs from the two eyes varies from neuron to neuron. At the extremes of this continuum are neurons that respond almost exclusively to the left or right eye; in the middle are those that respond equally well to both eyes. As in the case of orientation preference, vertical electrode penetrations tend to encounter neurons with similar ocular preference (or **ocular dominance**, as it is usually called), whereas tangential penetrations show gradual shifts in ocular dominance. And, like the arrangement of orientation preference, a movement of about a millimeter across the surface is required to sample the full complement of ocular dominance values (Figure 11.13). These shifts in ocular dominance result from the ocular segregation of the inputs from lateral geniculate nucleus within cortical layer IV (see Figure 11.10).

Although the modular arrangement of the visual cortex was first recognized on the basis of these orientation and ocular dominance columns, further work has shown that other stimulus features such as color, direction of motion, and spatial frequency also tend to be distributed in iterated patterns that are systematically related to each other (for example, orientation columns tend to intersect ocular dominance columns at right angles). In short, the striate cortex is composed of repeating units, or modules, that contain all the neuronal machinery necessary to analyze a small region of visual space for a variety of different stimulus attributes. As described in Box D in Chapter 8, a number of other cortical regions show a similar columnar arrangement of their processing circuitry.



Figure 11.13 Columnar organization of ocular dominance. (A) Cortical neurons in all layers vary in the strength of their response to the inputs from the two eyes, from complete domination by one eye to equal influence of the two eyes. (B) Tangential electrode penetration across the superficial cortical layers reveals a gradual shift in the ocular dominance of the recorded neurons from one eye to the other. In contrast, all neurons encountered in a vertical electrode penetration (other than those neurons that lie in layer IV) tend to have the same ocular dominance.

Division of Labor within the Primary Visual Pathway

In addition to being specific for input from one eye or the other, the layers in the lateral geniculate are also distinguished on the basis of cell size: Two ventral layers are composed of large neurons and are referred to as the **magnocellular layers**, while more dorsal layers are composed of small neurons and are referred to as the **parvocellular layers**. The magno- and parvocellular layers receive inputs from distinct populations of ganglion cells that exhibit corresponding differences in cell size. M ganglion cells that terminate in the magnocellular layers have larger cell bodies, more extensive dendritic fields, and larger-diameter axons than the P ganglion cells that terminate in the parvocellular layers of the lateral geniculate nucleus terminate on distinct populations of neurons located in separate strata within layer 4 of striate cortex. Thus the retinogeniculate pathway is composed of parallel **magnocellular and parvocellular streams** that convey distinct types of information to the initial stages of cortical processing.

The response properties of the M and P ganglion cells provide important clues about the contributions of the magno- and parvocellular streams to visual perception. M ganglion cells have larger receptive fields than P cells, and their axons have faster conduction velocities. M and P ganglion cells also differ in ways that are not so obviously related to their morphology. M cells respond transiently to the presentation of visual stimuli, while P cells respond in a sustained fashion. Moreover, P ganglion cells can transmit information about color, whereas M cells cannot. P cells convey color information because their receptive field centers and surrounds are driven by different classes of cones (i.e., cones responding with greatest sensitivity to

Box C Optical Imaging of Functional Domains in the Visual Cortex

The recent availability of optical imaging techniques has made it possible to visualize how response properties, such as the selectivity for edge orientation or ocular dominance, are mapped across the cortical surface. These methods generally rely on intrinsic signals (changes in the amount of light reflected from the cortical surface) that correlate with levels of neural activity. Such signals are thought to arise at least in part from local changes in the ratio of oxyhemoglobin and deoxyhemoglobin that accompany such activity, more active areas having a higher deoxyhemoglobin/oxyhemoglobin ratio (see also Box A in Chapter 1). This change can be detected when the cortical surface is illuminated with red light (605-700 nm). Under these conditions, active cortical regions absorb more light than less active ones. With the use of a sensitive video camera, and averaging over a number of trials (the changes are small, 1 or 2 parts per thousand), it is possible to visualize these differences and use them to map cortical patterns of activity (Figure A).

This approach has now been successfully applied to both striate and extrastriate areas in both experimental animals and human patients undergoing neurosurgery. The results emphasize that maps of stimulus features are a general principle of cortical organization. For example, orientation preference is mapped in a continuous fashion such that adjacent positions on the cortical surface tend to have only slightly shifted orientation preferences. However, there are points where continuity breaks down. Around these points, orientation preference is represented in a radial pattern resembling a pinwheel, covering the whole 180° of possible orientation values (Figure B).

This powerful technique can also be used to determine how maps for different stimulus properties are arranged relative to one another, and to detect additional maps such as that for direction of motion. A comparison of ocular dominance bands and orientation preference maps, for example, shows that pinwheel centers are generally located in the center of ocular dominance bands, and that the iso-orientation contours that emanate from the pinwheel centers run orthogonal to the borders of ocular dominance bands (Figure C). An orderly relationship between maps of orientation selectivity and direction selectivity has also been demonstrated. These systematic relationships between the functional maps that coexist within primary visual cortex are thought to ensure that all combinations of stimulus features (orientation, direction, ocular dominance, and spatial frequency) are analyzed for all regions of visual space.

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short-, medium-, or long-wavelength light). For example, some P ganglion cells have centers that receive inputs from long-wavelength ("red") sensitive cones and surrounds that receive inputs from medium-wavelength ("green") cones. Others have centers that receive inputs from "green cones" and surrounds from "red cones" (see Chapter 10). As a result, P cells are sensitive to differences in the wavelengths of light striking their receive field center

that this image shows only a small region of the overall map of orientation) (C) Comparison of optical image maps of orientation preference and ocular dominance in monkey visual cortex. The thick black lines represent the borders between ocular dominance columns. The thin gray lines represent the iso-orientation contours, which converge at orientation pinwheel centers (arrow). Iso-orientation contour lines generally intersect the borders of ocular dominance bands at right angles. (B from Bonhoeffer and Grinvald,

1993; C from Obermeyer and Blasdel, 1993.)

◄ Figure 11.14 Magno- and parvocellular streams. (A) Tracings of M and P ganglion cells as seen in flat mounts of the retina after staining by the Golgi method. M cells have large-diameter cell bodies and large dendritic fields. They supply the magnocellular layers of the lateral geniculate nucleus. P cells have smaller cell bodies and dendritic fields. They supply the parvocellular layers of the lateral geniculate nucleus. B) Photomicrograph of the human lateral geniculate nucleus showing the magnocellular and parvocellular layers. (A after Watanabe and Rodieck, 1989; B courtesy of T. Andrews and D. Purves.)

and surround. Although M ganglion cells also receive inputs from cones, there is no difference in the type of cone input to the receptive field center and surround; the center and surround of each M cell receptive field is driven by all cone types. The absence of cone specificity to center-surround antagonism makes M cells largely insensitive to differences in the wavelengths of light that strike their receptive field centers and surrounds, and they are thus unable to transmit color information to their central targets.

The contribution of the magno- and parvocellular streams to visual perception has been tested experimentally by examining the visual capabilities of monkeys after selectively damaging either the magno- or parvocellular layers of the lateral geniculate nucleus. Damage to the magnocellular layers has little effect on visual acuity or color vision, but sharply reduces the ability to perceive rapidly changing stimuli. In contrast, damage to the parvocellular layers has no effect on motion perception but severely impairs visual acuity and color perception. These observations suggest that the visual information conveyed by the parvocellular stream is particularly important for high spatial resolution vision—the detailed analysis of the shape, size, and color of objects. The magnocellular stream, on the other hand, appears critical for tasks that require high temporal resolution, such as evaluating the location, speed and direction of a rapidly moving object.

In addition to the magno- and parvocellular streams, a third distinct anatomical pathway—the **koniocellular**, or **K-cell pathway**—has been identified within the lateral geniculate nucleus. Neurons contributing to the Kcell pathway reside in the interlaminar zones that separate lateral geniculate layers; these neurons receive inputs from fine-caliber retinal axons and project in a patchy fashion to the superficial layers (layers II and III) of striate cortex. Although the contribution of the K-cell pathway to perception is not understood, it appears that some aspects of color vision, especially information derived from short-wavelength-sensitive cones, may be transmitted via the K-cell rather than the P-cell pathway. Why short-wavelength-sensitive cone signals should be processed differently from middle- and long-wavelength information is not clear, but the distinction may reflect the earlier evolutionary origin of the K-cell pathway (see Chapter 10).

The Functional Organization of Extrastriate Visual Areas

Anatomical and electrophysiological studies in monkeys have led to the discovery of a multitude of areas in the occipital, parietal, and temporal lobes that are involved in processing visual information (Figure 11.15). Each of these areas contains a map of visual space, and each is largely dependent on the primary visual cortex for its activation. The response properties of the neurons in some of these regions suggest that they are specialized for different aspects of the visual scene. For example, the **middle temporal area** (**MT**) contains neurons that respond selectively to the direction of a moving edge without regard to its color. In contrast, neurons in another cortical area called **V4** respond selectively to the color of a visual stimulus without regard to its direction of movement. These physiological findings are supported by behavioral evidence; thus, damage to area MT leads to a specific impairment in a monkey's ability to perceive the direction of motion in a stimulus pattern, while other aspects of visual perception remain intact.

Recent functional imaging studies have indicated a similar arrangement of visual areas within human extrastriate cortex. Using retinotopically restricted stimuli, it has been possible to localize at least 10 separate repre-



sentations of the visual field (Figure 11.16). One of these areas exhibits a large motion-selective signal, suggesting that it is the homologue of the motion-selective middle temporal area described in monkeys. Another area exhibits color-selective responses, suggesting that it may be similar to V4 in non-human primates. A role for these areas in the perception of motion and color, respectively, is further supported by evidence for increases in activity not only during the presentation of the relevant stimulus, but also during periods when subjects experience motion or color afterimages.

The clinical description of selective visual deficits after localized damage to various regions of extrastriate cortex also supports functional specialization of extrastriate visual areas in humans. For example, a well-studied patient who suffered a stroke that damaged the extrastriate region thought to be comparable to area MT in the monkey was unable to appreciate the motion of objects. The neurologist who treated her noted that she had difficulty in pouring tea into a cup because the fluid seemed to be "frozen." In addition, she could not stop pouring at the right time because she was unable to perceive when the fluid level had risen to the brim. The patient also had trouble following a dialogue because she could not follow the movements of the speaker's mouth. Crossing the street was potentially terrifying because she couldn't judge the movement of approaching cars. As the patient related, "When I'm looking at the car first, it seems far away. But **Figure 11.15** Subdivisions of the extrastriate cortex in the macaque monkey. (A) Each of the subdivisions indicated in color contains neurons that respond to visual stimulation. Many are buried in sulci, and the overlying cortex must be removed in order to expose them. Some of the more extensively studied extrastriate areas are specifically identified (V2, V3, V4, and MT). V1 is the primary visual cortex; MT is the middle temporal area. (B) The arrangement of extrastriate and other areas of neocortex in a flattened view of the monkey neocortex. There are at least 25 areas that are predominantly or exclusively visual in function, plus 7 other areas suspected to play a role in visual processing. (A after Maunsell and Newsome, 1987; B after Felleman and Van Essen, 1991.)



visual areas in the human brain using fMRI. (A,B) Lateral and medial views (respectively) of the human brain, illustrating the location of primary visual cortex (V1) and additional visual areas V2, V3, VP (ventral posterior area), V4, MT (middle temporal area), and MST (medial superior temporal area). (C) Unfolded and flattened view of retinotopically defined visual areas in the occipital lobe. Dark grey areas correspond to cortical regions that were buried in sulci; light regions correspond to regions that were located on the surface of gyri. Visual areas in humans show a close resemblance to visual areas originally defined in monkeys (compare with Figure 11.15). (After Sereno et al., 1995.)

then, when I want to cross the road, suddenly the car is very near." Her ability to perceive other features of the visual scene, such as color and form, was intact.

Another example of a specific visual deficit as a result of damage to extrastriate cortex is **cerebral achromatopsia**. These patients lose the ability to see the world in color, although other aspects of vision remain in good working order. The normal colors of a visual scene are described as being replaced by "dirty" shades of gray, much like looking at a poor quality black-and-white movie. Achromatopsic individuals know the normal colors of objects—that a school bus is yellow, an apple red—but can no longer see them. Thus, when asked to draw objects from memory, they have no difficulty with shapes but are unable to appropriately color the objects they have represented. It is important to distinguish this condition from the color blindness that arises from the congenital absence of one or more cone pigments in the retina (see Chapter 10). In achromatopsia, the three types of cones are functioning normally; it is damage to specific extrastriate cortical areas that renders the patient unable to use the information supplied by the retina. Based on the anatomical connections between visual areas, differences in electrophysiological response properties, and the effects of cortical lesions, a consensus has emerged that extrastriate cortical areas are organized into two largely separate systems that eventually feed information into cortical association areas in the temporal and parietal lobes (see Chapter 25). One system, called the ventral stream, includes area V4 and leads from the striate cortex into the inferior part of the temporal lobe. This system is thought to be responsible for high-resolution form vision and object recognition. The dortex into the parietal lobe. This system is thought to be responsible for spatial aspects of vision, such as the analysis of motion, and positional relationships between objects in the visual scene (Figure 11.17).

The functional dichotomy between these two streams is supported by observations on the response properties of neurons and the effects of selective cortical lesions. Neurons in the ventral stream exhibit properties that are important for object recognition, such as selectivity for shape, color, and texture. At the highest levels in this pathway, neurons exhibit even greater selectivity, responding preferentially to faces and objects (see Chapter 25). In contrast, those in the dorsal stream are not tuned to these properties, but show selectivity for direction and speed of movement. Consistent with this interpretation, lesions of the parietal cortex severely impair an animal's ability to distinguish objects on the basis of their position, while having little effect on its ability to perform object recognition tasks. In contrast, lesions of the inferotemporal cortex produce profound impairments in the ability to perform recognition tasks but no impairment in spatial tasks. These effects are remarkably similar to the syndromes associated with damage to the parietal and temporal lobe in humans (see Chapters 25 and 26).

What, then, is the relationship between these "higher-order" extrastriate visual pathways and the magno- and parvocellular pathways that supply the primary visual cortex? Not long ago, it seemed that these intracortical pathways were simply a continuation of the geniculostriate pathways—that is, the magnocellular pathway provided input to the dorsal stream and the parvocellular pathway provided input to the ventral stream. However, more recent work has indicated that the situation is more complicated. The temporal pathway clearly has access to the information conveyed by both the magno- and parvocellular streams; and the parietal pathway, while dominated by inputs from the magnocellular stream, also receives inputs from the parvocellular streams appear to be the rule in complex visual perceptions.

Summary

Distinct populations of retinal ganglion cells send their axons to a number of central visual structures that serve different functions. The most important projections are to the pretectum for mediating the pupillary light reflex, to the hypothalamus for the regulation of circadian rhythms, to the superior colliculus for the regulation of eye and head movements, and—most important of all—to the lateral geniculate nucleus for mediating vision and visual perception. The retinogeniculostriate projection (the primary visual pathway) is arranged topographically such that central visual structures contain an organized map of the contralateral visual field. Damage anywhere along the primary visual pathway, which includes the optic nerve, optic tract, lateral geniculate nucleus, optic radiation, and striate cortex, results in a loss of vision confined to a predictable region of visual space. Compared to retinal



Figure 11.17 The visual areas beyond the striate cortex are broadly organized into two pathways: a ventral pathway that leads to the temporal lobe, and a dorsal pathway that leads to the parietal lobe. The ventral pathway plays an important role in object recognition, the dorsal pathway in spatial vision.

ganglion cells, neurons at higher levels of the visual pathway become increasingly selective in their stimulus requirements. Thus, most neurons in the striate cortex respond to light–dark edges only if they are presented at a certain orientation; some are selective for the length of the edge, and others to movement of the edge in a specific direction. Indeed, a point in visual space is related to a set of cortical neurons, each of which is specialized for processing a limited set of the attributes in the visual stimulus. The neural circuitry in the striate cortex also brings together information from the two eyes; most cortical neurons (other than those in layer IV, which are segregated into eye-specific columns) have binocular responses. Binocular convergence is presumably essential for the detection of binocular disparity, an important component of depth perception. The primary visual pathway is composed of separate functional streams that convey information from different types of retinal ganglion cells to the initial stages of cortical processing. The magnocellular stream conveys information that is critical for the detection of rapidly changing stimuli, the parvocellular stream mediates high acuity vision and appears to share responsibility for color vision with the koniocellular stream. Finally, beyond striate cortex, parcellation of function continues in the ventral and dorsal streams that lead to the extrastriate and association areas in the temporal and parietal lobes, respectively. Areas in the inferotemporal cortex are especially important in object recognition, whereas areas in the parietal lobe are critical for understanding the spatial relations between objects in the visual field.

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