

Figure 21–4 A visual scene is analyzed at three levels. Simple attributes of the visual environment are analyzed (low-level processing), and these low-level features are then used to parse the visual scene (intermediate-level processing): Local visual features are assembled into surfaces, objects are segregated from background (surface segmentation), local orientation

is integrated into global contours (contour integration), and surface shape is identified from shading and kinematic cues. Finally, surfaces and contours are used to identify the object (high-level processing). (M.C. Escher's "Day and Night". © 2020 The M.C. Escher Company—The Netherlands. All rights reserved. www.mcescher.com)



Priming image for Figure 21-3

underlying nerve damage or occlusion (ranging from optic nerve degeneration, such as due to multiple sclerosis, to tumors, strokes, or physical trauma).

Beyond the optic chiasm, the axons from nasal and temporal hemiretinas carrying input from one hemifield join in the optic tract, which extends to the lateral geniculate nucleus (LGN) of the thalamus. The LGN in primates consists of six primary layers: four parvocellular (Latin *Parvus*, small) and two magnocellular, each paired with a thin but dense intercalated or koniocellular (Greek *konio*, dust) layer (see Figure 21–14). The term “koniocellular” refers to the substantially smaller cell bodies in these layers relative to those of magnocellular or parvocellular layers. The parallel channels established in the retinas remain anatomically segregated through the LGN. Parvocellular layers get input from the midget retinal ganglion cells, which are the most numerous in the primate retina (~70%) and carry red-green opponent information (Chapter 22). Magnocellular layers get achromatic contrast information from the parasol ganglion cells (~10%). Koniocellular layers get input from the small and large bistratified ganglion cells, carrying blue-yellow information, that together make up the third most populous set of retinal projections to the LGN (~8%). Koniocellular layers also get inputs from a number of other numerically much smaller classes of retinal ganglion cells.

Each geniculate layer receives input from either the ipsilateral or the contralateral eye (see Figure 21–12) but is aligned so as to come from a matching region of the contralateral hemifield. Thus, they form a set of concordant maps stacked atop one another. The thalamic neurons then relay retinal information to

the primary visual cortex. But the LGN is not simply a relay; the retinal information it receives can be strongly modulated by attention and arousal through inhibitory connections to this brain region and by feedback from the visual cortex.

The primary visual pathway is also called the geniculostriate pathway (Figure 21–6A) because it passes through the LGN on its way to the primary visual cortex (V1), also known as the striate cortex because of the myelin-rich stripe that runs through its middle layers. A second pathway extends from the retina to the pretectal area of the midbrain, where neurons mediate the pupillary reflexes that control the amount of light entering the eyes (Figure 21–6B). A third pathway from the retina runs to the superior colliculus and is important in controlling eye movements. This pathway continues to the pontine formation in the brain stem and then to the extraocular motor nuclei (Figure 21–6C).

Each LGN projects to the primary visual cortex through a pathway known as the optic radiation. These afferent fibers form a complete neural map of the contralateral visual field in the primary visual cortex. Beyond the striate cortex lie the extrastriate areas, a set of higher-order visual areas that are also organized as neural maps of the visual field. The preservation of the spatial arrangement of inputs from the retina is called retinotopy, and a neural map of the visual field is described as retinotopic or having a retinotopic frame of reference.

The primary visual cortex constitutes the first level of cortical processing of visual information. From there, information is transmitted over two major pathways. A ventral pathway into the temporal lobe carries information about what the stimulus is, and a dorsal

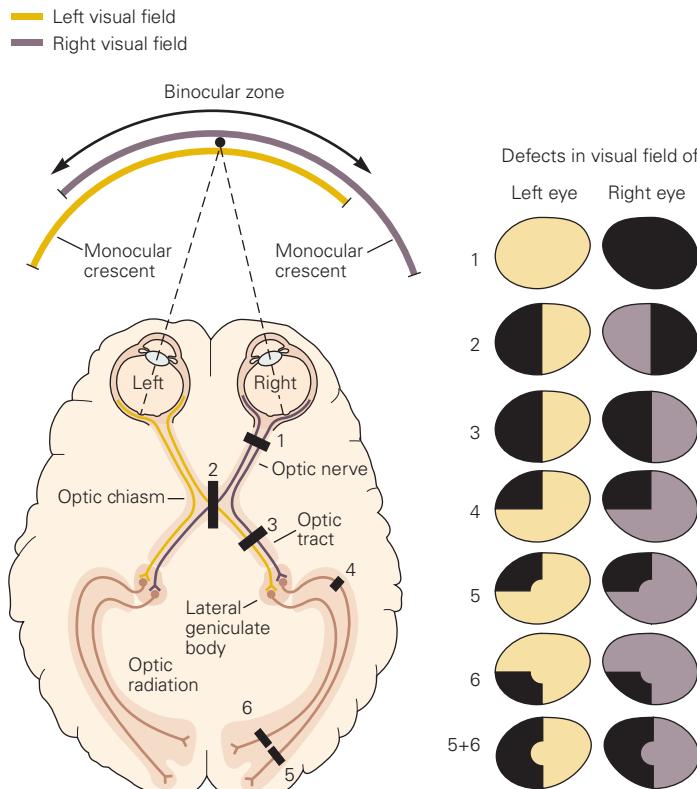


Figure 21–5 Representation of the visual field along the visual pathway. Each eye sees most of the visual field, with the exception of a portion of the peripheral visual field known as the monocular crescent. The axons of retinal neurons (ganglion cells) carry information from each visual hemifield along the optic nerve up to the optic chiasm, where fibers from the nasal hemiretina cross to the opposite hemisphere. Fibers from the temporal hemiretina stay on the same side, joining the fibers from the nasal hemiretina of the contralateral eye to form the optic tract. The optic tract carries information from the opposite visual hemifield originating in both eyes and projects into the lateral geniculate nucleus. Cells in this nucleus send their axons along the optic radiation to the primary visual cortex.

Lesions along the visual pathway produce specific visual field deficits, as shown on the right:

1. A lesion of an optic nerve causes a total loss of vision in one eye.

pathway into the parietal lobe carries information about where the stimulus is, information that is critical for guiding movement.

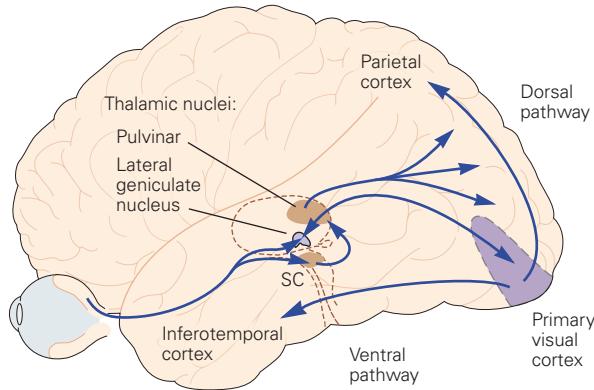
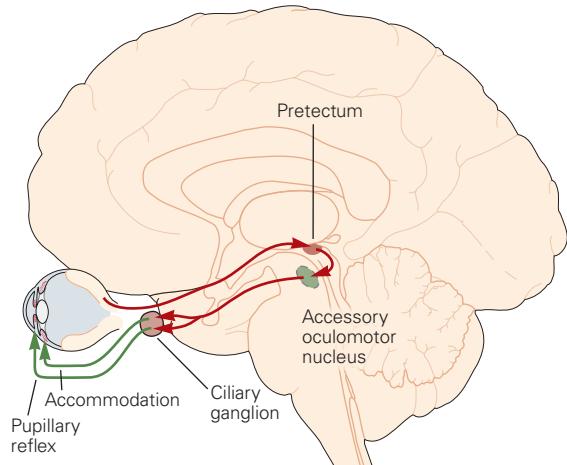
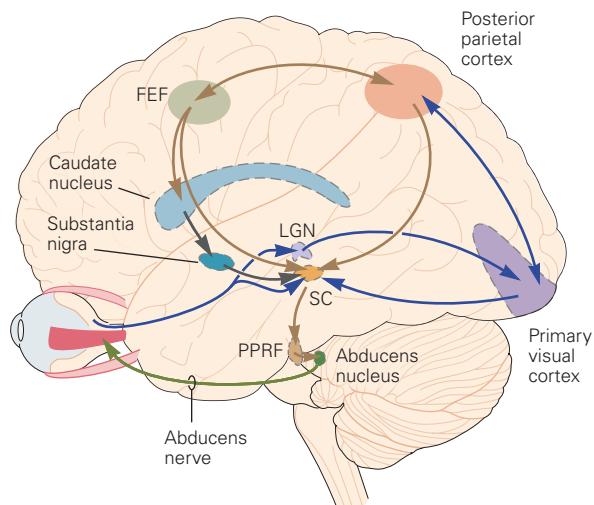
A major fiber bundle called the corpus callosum connects the two hemispheres, transmitting information across the midline. The primary visual cortex in each hemisphere represents slightly more than half the visual field, with the two hemifield representations overlapping at the vertical meridian. One of the functions of the corpus callosum is to unify the perception

2. A lesion of the optic chiasm causes a loss of vision in the temporal half of each visual hemifield (bitemporal hemianopsia).
3. A lesion of the optic tract causes a loss of vision in the opposite half of the visual hemifield (contralateral hemianopsia).
4. A lesion of the optic radiation fibers that curve into the temporal lobe (Meyer's loop) causes loss of vision in the upper quadrant of the contralateral visual hemifield in both eyes (upper contralateral quadrantic anopsia).
- 5, 6. Partial lesions of the visual cortex lead to deficits in portions of the contralateral visual hemifield. For example, a lesion in the upper bank of the calcarine sulcus (5) causes a partial deficit in the inferior quadrant, while a lesion in the lower bank (6) causes a partial deficit in the superior quadrant. The central area of the visual field tends to be unaffected by cortical lesions because of the extent of the representation of the fovea and the duplicate representation of the vertical meridian in the hemispheres.

of objects spanning the vertical meridian by linking the cortical areas that represent opposite hemifields.

Form, Color, Motion, and Depth Are Processed in Discrete Areas of the Cerebral Cortex

In the late 19th and early 20th centuries, the cerebral cortex was differentiated into discrete regions by the anatomist Korbinian Brodmann and others using

A Visual processing**B Pupillary reflex and accommodation****C Eye movement (horizontal)**

anatomical criteria. The criteria included the size, shape, and packing density of neurons in the cortical layers and the thickness and density of myelin. The functionally distinct cortical areas we have considered heretofore correspond only loosely to Brodmann's classification. The primary visual cortex (V1) is identical to Brodmann's area 17. In the extrastriate cortex, the secondary visual area (V2) corresponds to area 18. Beyond that, however, area 19 contains several functionally distinct areas that generally cannot be defined by anatomical criteria.

The number of functionally discrete areas of visual cortex varies between species. Macaque monkeys have more than 30 areas. Although not all visual areas in humans have yet been identified, the number is likely to be at least as great as in the macaque. If one includes oculomotor areas and prefrontal areas contributing to visual memory, almost half of the cerebral cortex is involved with vision. Functional magnetic resonance imaging (fMRI) has made it possible to establish homologies between the visual areas of the macaque and human brains (Figure 21–7). Based on pathway tracing studies in monkeys, we now appreciate that these areas are organized in functional streams (Figure 21–7B).

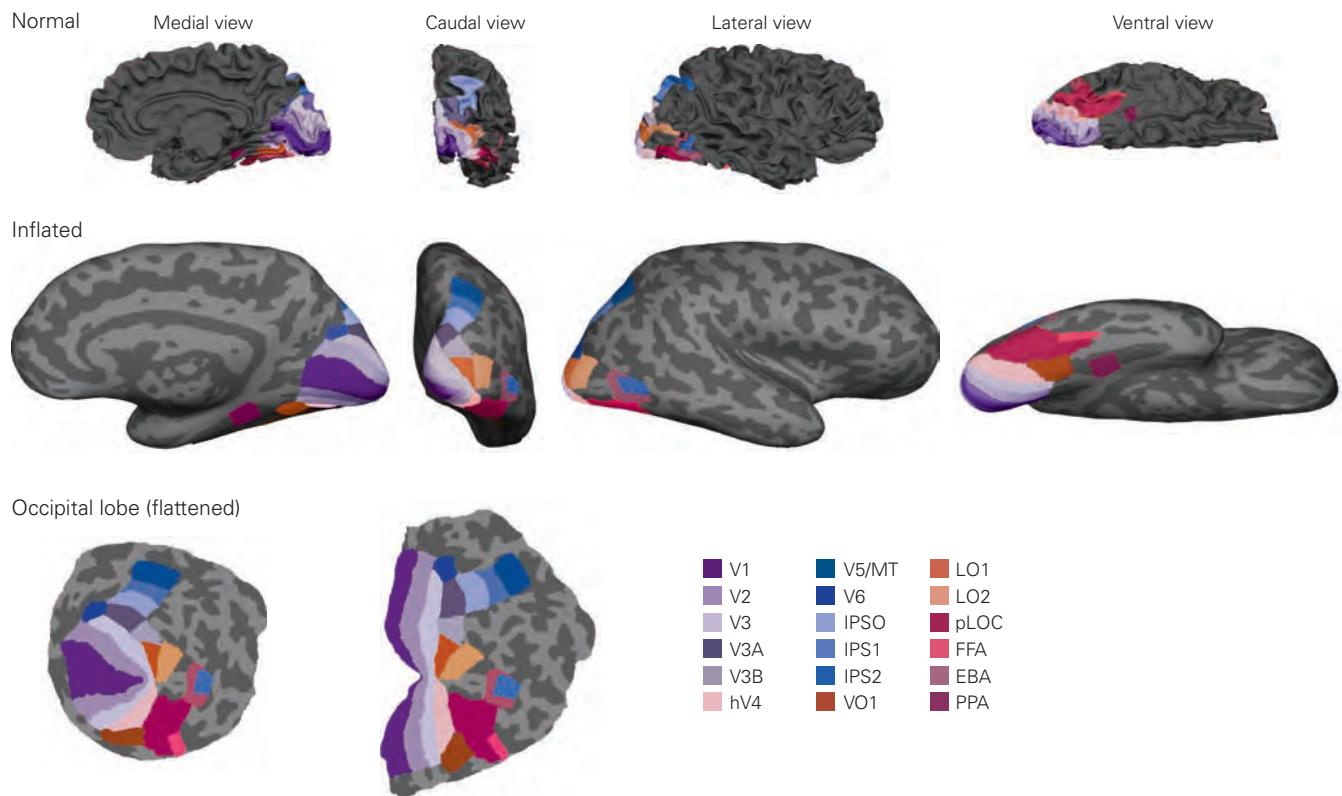
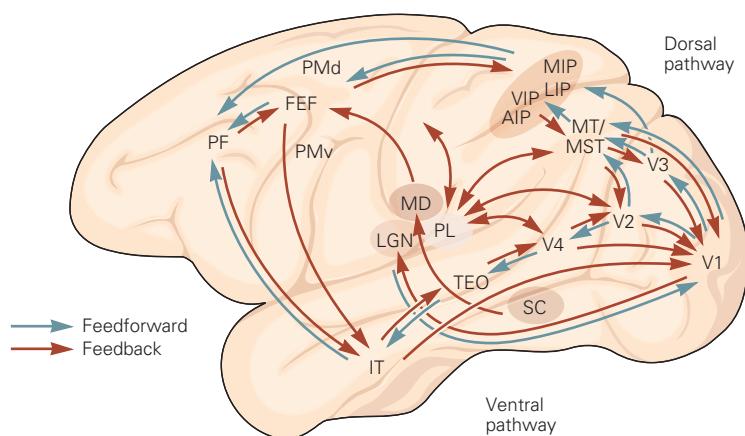
The visual areas of cortex can be differentiated by the functional properties of their neurons. Studies of

Figure 21–6 Pathways for visual processing, pupillary reflex and accommodation, and control of eye position.

A. Visual processing. The eye sends information first to thalamic nuclei, including the lateral geniculate nucleus and pulvinar, and from there to cortical areas. Cortical projections go forward from the primary visual cortex to areas in the parietal lobe (the dorsal pathway, which is concerned with visually guided movement) and areas in the temporal lobe (the ventral pathway, which is concerned with object recognition). The pulvinar also serves as a relay between cortical areas to supplement their direct connections. (Abbreviation: SC, superior colliculus).

B. Pupillary reflex and accommodation. Light signals are relayed through the midbrain pretectum, to preganglionic parasympathetic neurons in the accessory oculomotor (Edinger-Westphal) nucleus, and out through the parasympathetic outflow of the oculomotor nerve to the ciliary ganglion. Postganglionic neurons innervate the smooth muscle of the pupillary sphincter, as well as the muscles controlling the lens.

C. Eye movement. Information from the retina is sent to the superior colliculus (SC) directly along the optic nerve and indirectly through the geniculostriate pathway to cortical areas (primary visual cortex, posterior parietal cortex, and frontal eye fields) that project back to the superior colliculus. The colliculus projects to the pons (PPRF), which then sends control signals to oculomotor nuclei, including the abducens nucleus, which controls lateral movement of the eyes. (Abbreviations: FEF, frontal eye field; LGN, lateral geniculate nucleus; PPRF, para-median pontine reticular formation.)

A Cortical visual areas in humans**B** Visual pathways in the macaque monkey

such functional properties have revealed that the visual areas are organized in two hierarchical pathways, a ventral pathway involved in object recognition and a dorsal pathway dedicated to the use of visual information for guiding movements. The ventral or object-recognition pathway extends from the primary visual cortex to the temporal lobe; it is described in detail in Chapter 24. The dorsal or movement-guidance pathway connects the primary visual cortex with the parietal lobe and then with the frontal lobes.

The pathways are interconnected so that information is shared. For example, movement information in the dorsal pathway can contribute to object recognition through kinematic cues. Information about movements in space derived from areas in the dorsal pathway is therefore important for the perception of object shape and is fed into the ventral pathway.

All connections between cortical areas are reciprocal—each area sends information back to the areas from which it receives input. These feedback connections provide information about cognitive functions, including spatial attention, stimulus expectation, and emotional content, to earlier levels of visual

processing. The pulvinar in the thalamus serves as a relay between cortical areas (see Figure 21–7B).

The dorsal pathway courses through the parietal cortex, a region that uses visual information to direct the movement of the eyes and limbs, that is, for visuomotor integration. The lateral intraparietal area, named for its location in the intraparietal sulcus, is involved in representing points in space that are the targets of eye movements or reaching. Patients with lesions of parietal areas fail to attend to objects on one side of the body, a syndrome called *unilateral neglect* (see Figure 59–1 in Chapter 59).

The ventral pathway extends into the temporal lobe. The inferior temporal cortex stores information about the shapes and identities of objects; one portion represents faces, for damage to that region results in the inability to recognize faces (*prosopagnosia*).

The dorsal and ventral pathways each comprise a hierarchical series of areas that can be delineated by several criteria. First, at many relays, the array of inputs forms a map of the visual hemifield. The boundaries of these maps can be used to demarcate the boundaries of visual areas. This is particularly useful at early levels of the pathway where the receptive fields of neurons

Figure 21–7 Visual pathways in the cerebral cortex.

A. Functional magnetic resonance imaging shows areas of the human cerebral cortex involved in visual processing. The top row shows areas on the gyri and sulci of a normal view of a brain; the middle row shows “inflated” views of the brain following a computational process that simulates inflating the brain like a balloon so as to stretch out the “wrinkles” of gyri and sulci into a smooth surface while minimizing local distortions. Light and dark gray regions identify gyri and sulci, respectively; the bottom row shows a two-dimensional representation of the occipital lobe (left) and a representation with less distortion by making a cut along the calcarine fissure. Different approaches are required for demarcating different functional areas. Retinotopic areas, by definition, contain continuous maps of visual space and are identified using stimuli such as rotating spirals or expanding circles that sweep through visual space. Maps in adjacent cortical areas run in opposite directions on the cortical surface and meet along boundaries of local mirror reversals. These mirror reversals can be used to identify area boundaries and thus demarcate each area. These retinotopic areas, including early visual areas V1, V2, and V3, and areas V3A, V3B, V6, hV4, VO1, LO1, LO2, and V5/MT, share boundaries in pairs; these boundaries converge (at the representation of the fovea) at the occipital pole. A different approach, identifying loci of attention, is used to map areas IPS1 and IPS2. Yet further sets of approaches or responsiveness to specific attributes or classes of objects (such as faces) are used for less strictly retinotopic areas. Functional specificity has been demonstrated for a number of visual areas: VO1 is implicated in color processing, the lateral occipital complex (LO2, pLOC) codes object shape, fusiform face area (FFA)

codes faces, the parahippocampal place area (PPA) responds more strongly to places than to objects, the extrastriate body area (EBA) responds more strongly to body parts than objects, and V5/MT is involved in motion processing. Areas in the intraparietal sulcus (IPS1 and IPS2) are involved in control of spatial attention and saccadic eye movements. (Images courtesy of V. Piech, reproduced with permission.)

B. In the macaque monkey, V1 is located on the surface of the occipital lobe and sends axons in two pathways. A dorsal pathway courses through a number of areas in the parietal lobe and into the frontal lobe and mediates attentional control and visually guided movements. A ventral pathway projects through V4 into areas of the inferior temporal cortex and mediates object recognition. In addition to feedforward pathways extending from primary visual cortex into the temporal, parietal, and frontal lobes (blue arrows), reciprocal or feedback pathways run in the opposite direction (red arrows). Feed-forward and feedback can operate directly, between cortical areas, or indirectly, via the thalamus, in particular the pulvinar, which acts as a relay between cortical areas. The subcortical pathways involved include thalamic nuclei—the lateral geniculate nucleus (LGN), pulvinar nucleus (PL), and mediodorsal nucleus (MD)—and the superior colliculus (SC). (Abbreviations: AIP, anterior intraparietal area; FEF, frontal eye field; IT, inferior temporal cortex; LIP, lateral intraparietal area; MIP, medial intraparietal area; MT, middle temporal area; PF, prefrontal cortex; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; TEO, posterior division of area IT; V1, primary visual cortex, Brodmann's area 17; V2, secondary visual area, Brodmann's area 18; V3, V4, third and fourth visual areas; VIP, ventral intraparietal area.)

are small and visuotopic maps are precisely organized (see the next section for the definition of receptive field). At higher levels, however, the receptive fields become larger, the maps less precise, and visuotopic organization is therefore a less reliable basis to delineate the boundaries of an area.

Another means to differentiate one area from another, as shown by experiments in monkeys, depends upon the distinctive functional properties exhibited by the neurons in each area. The clearest example of this is an area in the dorsal pathway, the middle temporal area (MT or V5), which contains neurons with a strong selectivity for the direction of movement across their receptive fields. Consistent with the idea that the middle temporal area is involved in the analysis of motion, lesions of this area produce deficits in the ability to track moving objects.

A classical view of the organization of visual cortical areas is a hierarchical one, where the areas at the bottom of the hierarchy, such as V1 and V2, represent the visual primitives of orientation, direction of movement, depth, and color. In this view, the top of the ventral pathway's hierarchy would represent whole objects, with the areas in between representing intermediate level vision. This idea of "complexification" along the hierarchy suggests a mapping between the levels of visual perception and stages in the sequence of cortical areas. But more recent findings indicate a more complex story, where even the primary visual cortex plays a role in intermediate-level vision, and neurons in the higher areas may process information on components of objects. Moreover, as shown in Figure 21–7, one also has to take into account the fact that there is a powerful reverse flow of information, or feedback, from the "higher" to the "lower" cortical areas. As will be described in Chapter 23, this reverse direction of information contains higher order "top-down" cognitive influences including attention, object expectation, perceptual task, perceptual learning, and efference copy. Top-down influences may play a role in scene segmentation, object relationships, and perception of object details, as well as object recognition itself.

The Receptive Fields of Neurons at Successive Relays in the Visual Pathway Provide Clues to How the Brain Analyzes Visual Form

In 1906, Charles Sherrington coined the term *receptive field* in his analysis of the scratch withdrawal reflex: "The whole collection of points of skin surface from which the scratch-reflex can be elicited is termed the receptive field of that reflex." When it became possible

to record from single neurons in the eye, H. Keffer Hartline applied the concept of the receptive field in his study of the retina of the horseshoe crab, *Limulus*: "The region of the retina which must be illuminated in order to obtain a response in any given fiber . . . is termed the receptive field of that fiber." In the visual system, a neuron's receptive field represents a small window on the visual field (Figure 21–8).

But responses to only one spot of light yielded a limited understanding of a cell's receptive field. Using two small spots of light, both Hartline and Stephen Kuffler, who studied the mammalian retina, found an inhibitory surround or lateral inhibitory region in the receptive field. In 1953, Kuffler observed that "not only the areas from which responses can actually be set up by retinal illumination may be included in a definition of the receptive field but also all areas which show a functional connection, by an inhibitory or excitatory effect on a ganglion cell." Kuffler thus demonstrated that the receptive fields of retinal ganglion cells have functionally distinct subareas. These receptive fields have a center-surround organization and fall into one of two categories: *on-center* and *off-center*. Later work demonstrated that neurons in the LGN have similar receptive fields.

The on-center cells fire when a spot of light is turned on within a circular central region. Off-center cells fire when a spot of light in the center of their receptive field is turned off. The surrounding annular region has the opposite sign. For on-center cells, a light stimulus anywhere in the annulus surrounding the center produces a response when the light is turned off, a response termed *on-center, off-surround*. The center and surround areas are mutually inhibitory (Figure 21–9). When both center and surround are illuminated with diffuse light, there is little or no response. Conversely, a light-dark boundary across the receptive field produces a brisk response. Because these neurons are most sensitive to borders and contours—to differences in illumination as opposed to uniform surfaces—they encode information about contrast in the visual field.

The size on the retina of a receptive field varies both according to the field's *eccentricity*—its position relative to the fovea, the central part of the retina where visual acuity is highest—and the position of neurons along the visual pathway. Receptive fields with the same eccentricity are relatively small at early levels in visual processing and become progressively larger at later levels. The size of the receptive field is expressed in terms of degrees of visual angle; the entire visual field covers nearly 180° (Figure 21–10A). In early relays of visual processing, the receptive fields near the fovea are the smallest. The receptive

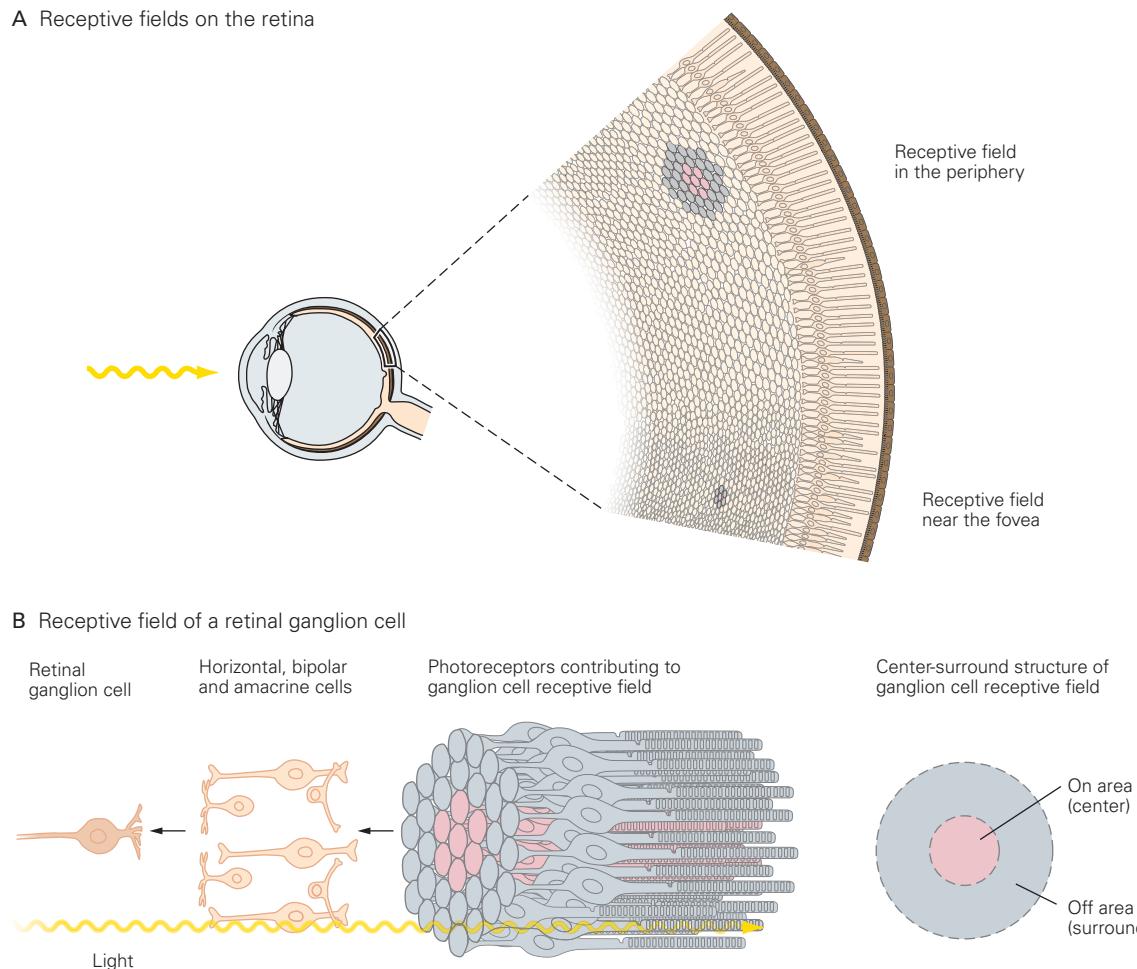


Figure 21–8 Receptive fields of retinal ganglion cells in relation to photoreceptors.

A. The number of photoreceptors contributing to the receptive field of a retinal ganglion cell varies depending on the location of the receptive field on the retina. A cell near the fovea receives input from fewer receptors covering a smaller area,

whereas a cell farther from the fovea receives input from many more receptors covering a larger area (see Figure 21–10).

B. Light passes through nerve cell layers to reach the photoreceptors at the back of the retina. Signals from the photoreceptors are then transmitted by neurons in the outer and inner nuclear layers to a retinal ganglion cell.

fields for retinal ganglion cells that monitor portions of the fovea subtend approximately 0.1° , whereas those in the visual periphery can be a couple of orders of magnitude larger.

The amount of cortex dedicated to a degree of visual space changes with eccentricity. More area of cortex is dedicated to the central part of the visual field, where the receptive fields are smallest and the visual system has the greatest spatial resolution (Figure 21–10C).

Receptive-field properties change from relay to relay along a visual pathway. By determining these properties, one can assay the function of each relay nucleus and how visual information is progressively

analyzed by the brain. For example, the change in receptive-field structure that occurs between the LGN and cerebral cortex reveals an important mechanism in the brain's analysis of visual form. The key property of the form pathway is selectivity for the orientation of contours in the visual field. This is an emergent property of signal processing in primary visual cortex; it is not a property of the cortical input but is generated within the cortex itself.

Whereas retinal ganglion cells and neurons in the LGN have concentric center-surround receptive fields, those in the cortex, although equally sensitive to contrast, also analyze contours. David Hubel and Torsten Wiesel discovered this characteristic in 1958

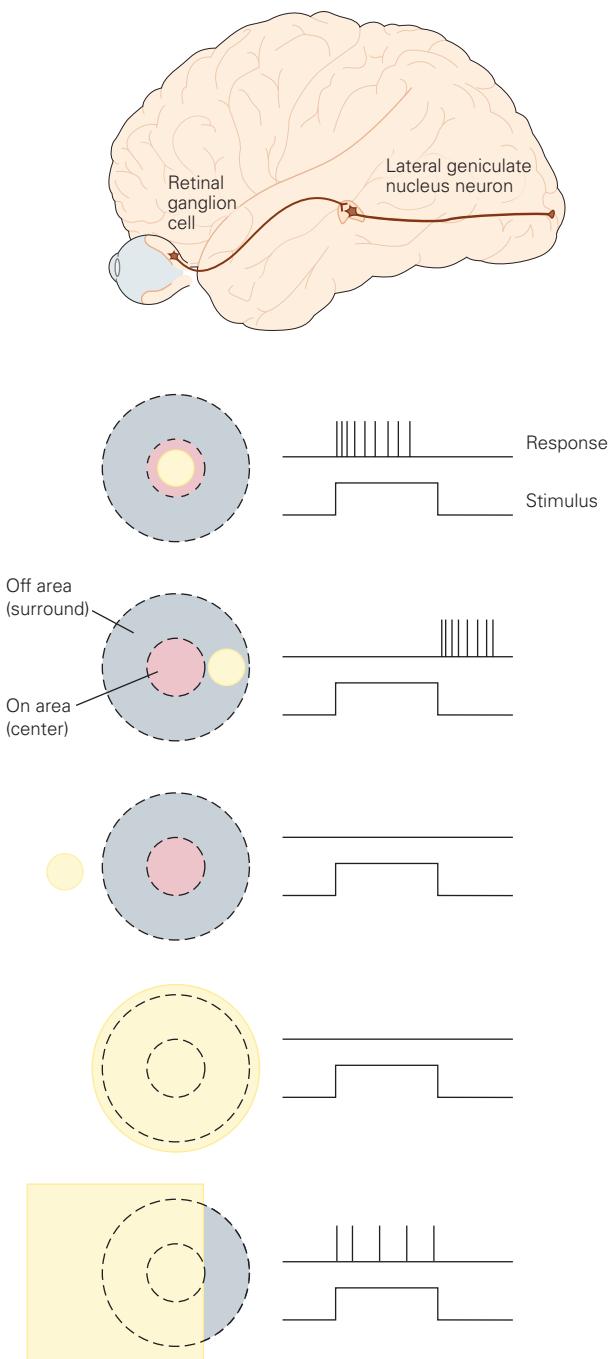


Figure 21-9 Receptive fields of neurons at early relays of visual pathways. A circular symmetric receptive field with mutually antagonistic center and surround is characteristic of retinal ganglion cells and neurons in the lateral geniculate nucleus of the thalamus. The center can respond to the turning on or turning off of a spot of light (yellow) depending on whether the receptive field belongs to an “on-center” or “off-center” class, respectively. The surround has the opposite response. Outside the surround, there is no response to light, thus defining the receptive field boundary. The response is weak when light covers both the center and surround, so these neurons respond optimally to contrast (a light–dark boundary) in the visual field.

while studying what visual stimuli provoked activity in neurons in the primary visual cortex. While showing an anesthetized animal slides containing a variety of images, they recorded extracellularly from individual neurons in the visual cortex. As they switched from one slide to another, they found a neuron that produced a brisk train of action potentials. The cell was responding not to the image on the slide but to the edge of the slide as it was moved into position.

The Visual Cortex Is Organized Into Columns of Specialized Neurons

The dominant feature of the functional organization of the primary visual cortex is the visuotopic organization of its cells: the visual field is systematically represented across the surface of the cortex (Figure 21-11A).

In addition, cells in the primary visual cortex with similar functional properties are located close together in columns that extend from the surface of the cortex to the white matter. The columns are concerned with the functional properties that are analyzed in any given cortical area and thus reflect the functional role of that area in vision. The properties that are developed in the primary visual cortex include orientation specificity and the integration of inputs from the two eyes, which is measured as the relative strength of input from each eye, or ocular dominance.

Ocular-dominance columns reflect the segregation of thalamocortical inputs arriving from different layers of the LGN. Alternating layers of this nucleus receive input from retinal ganglion cells located in either the ipsilateral or contralateral retina (Figure 21-12). This segregation is maintained in the inputs from the LGN to the primary visual cortex, producing the alternating left-eye and right-eye ocular dominance bands (Figure 21-11B).

Cells with similar orientation preferences are also grouped into columns. Across the cortical surface, there is a regular clockwise and counterclockwise cycling of orientation preference, with the full 180° cycle repeating every 750 µm (Figure 21-11C). Likewise, the left- and right-eye dominance columns alternate with a periodicity of 750 to 1,000 µm. One full cycle of orientation columns, or a full pair of left- and right-eye dominance columns, is called a *hypercolumn*. The orientation and ocular dominance columns at each point on the cortical surface are locally roughly orthogonal to each other. Thus, a cortical patch one hypercolumn in extent contains all possible combinations of orientation preference and left- and right-eye dominance.