

depends on the point of recombination. In tritanopes, the loss of S-cone function arises from mutations in the S-pigment gene.

Rod and Cone Circuits Merge in the Inner Retina

For vision under low-light conditions, the mammalian retina has an ON bipolar cell that is exclusively connected to rods (see Figure 22–3B). By collecting inputs from up to 50 rods, this rod bipolar cell can pool the effects of dispersed single-photon absorptions in a small patch of retina. There is no corresponding OFF bipolar cell dedicated to rods.

Unlike all other bipolar cells, the rod bipolar cell does not contact ganglion cells directly but instead excites a dedicated neuron, the AII amacrine cell. This amacrine cell receives inputs from several rod bipolar cells and conveys its output to cone bipolar cells. It provides excitatory signals to ON bipolar cells through gap junctions as well as glycinergic inhibitory signals to OFF bipolar cells. These cone bipolar cells in turn excite ON and OFF ganglion cells, as described earlier. Thus, the rod signal is fed into the cone system after a detour that produces the appropriate signal polarities for the ON and OFF pathways. The purpose of the added interneurons may be to allow greater pooling of rod signals than of cone signals.

Rod signals also enter the cone system through two other pathways. Rods can drive neighboring cones directly through electrical junctions, and they make connections with an OFF bipolar cell that services primarily cones. Once the rod signal has reached the cone bipolars through these pathways, it can take advantage of the same intricate circuitry of the inner retina. Thus, the rod system of the mammalian retina may have been an evolutionary afterthought added to the cone circuits.

The Retina's Sensitivity Adapts to Changes in Illumination

Vision operates under many different lighting conditions. The intensity of the light coming from an object depends on the intensity of the ambient illumination and the fraction of this light reflected by the object's surface, called the *reflectance*. The range of intensities encountered in a day is enormous, with variation spanning 10 orders of magnitude, but most of this variation is useless for the purpose of guiding behavior.

The illumination intensity varies by about nine orders of magnitude, mostly because our planet turns about its axis once a day, while the object reflectance

varies much less, by about one order of magnitude in a typical scene. But this reflectance is the interesting quantity for vision, for it characterizes objects and distinguishes them from the background. In fact, our visual system is remarkably good at calculating surface reflectances independently of ambient illumination (Figure 22–18).

With an overall increase in ambient illumination, all points in the visual scene become brighter by the same factor. If the eye could simply reduce its sensitivity by that same factor, the neural representation of the image would remain unchanged at the level of the ganglion cells and could be processed by the rest of the brain in the same way as before the change in illumination. Moreover, the retinal ganglion cells would only need to encode the 10-fold range of image intensities owing to the different object reflectances, instead of the 10-billion-fold range that includes variations in ambient illumination. Some of this adjustment in sensitivity is performed by the pupil, which contracts in bright light, reducing retinal illumination by up to a factor of 10. In addition, the retina itself performs an automatic gain control, called *light adaptation*, that approaches the ideal normalization we have imagined here.

Light Adaptation Is Apparent in Retinal Processing and Visual Perception

When flashes of light of different intensity are presented with a constant background illumination, the responses of a retinal ganglion cell fit a sigmoidal curve (Figure 22–19A). The weakest flashes elicit no response, a graded increase in flash intensity elicits graded responses, and the brightest flashes elicit saturation. When the background illumination is increased, the response curve maintains the same shape but is shifted to higher flash intensities. Compensating for the increase in background illumination, the ganglion cell is now less sensitive to light variations: In the presence of a higher background, a larger change is needed to cause the same response. This lateral shifting of the stimulus–response relationship is a hallmark of light adaptation in the retina.

The consequences of this gain change for human visual perception are readily apparent in psychophysical experiments. When human subjects are asked to detect a flash in a background field of constant illumination, detection on a brighter background necessitates a brighter flash (Figure 22–19B). Under the ideal gain-control mechanism discussed earlier, two stimuli would produce the same response if they caused the same fractional change from the background intensity. In that case, the threshold flash intensity should

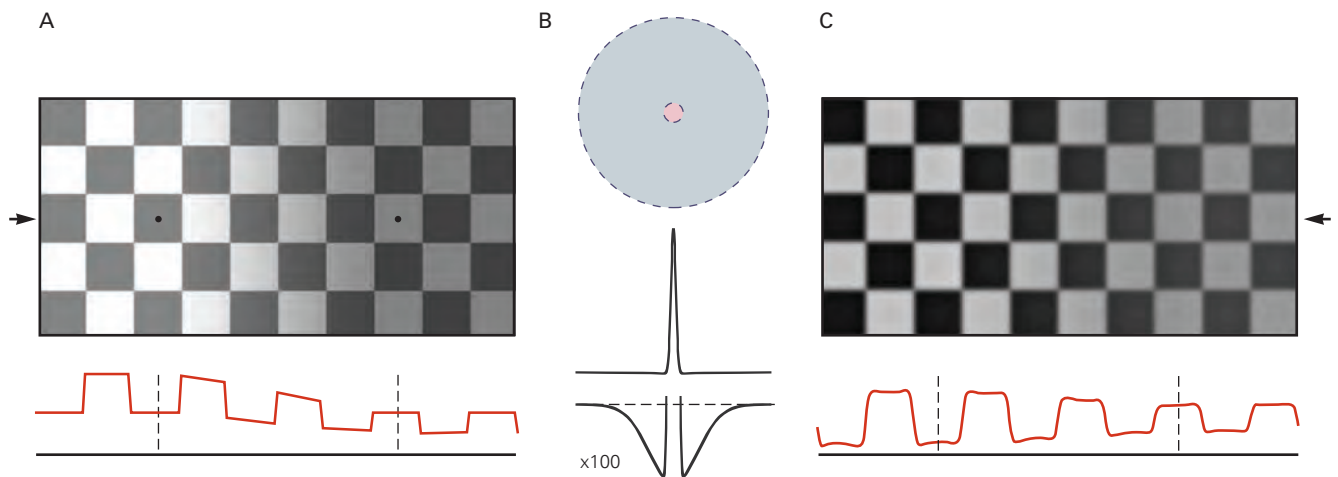


Figure 22-18 A brightness illusion.

A. The two tiles marked with small dots appear to have different color but actually reflect the same light intensity. (To see this, fold the page so they touch.) The trace underneath plots a profile of light intensity at the level of the arrowheads. Your visual system interprets this retinal image as a regular tile pattern under spatially varying illumination with a diffuse shadow in the right half. Under that interpretation, the right tile must have a lighter color than the left, which is what you perceive. This process is automatic and requires no conscious analysis.

B. Retinal processing contributes to the perception of “lightness” by discounting the shadow’s smooth gradients of illumination and accentuating the sharp edges between

checkerboard fields. The receptive field for a visual neuron with an excitatory center and inhibitory surround is shown at the top. As shown in a hundredfold magnification at the bottom, the surround is weak but extends over a much larger area than the center.

C. The result when a population of visual neurons with receptive fields as in **B** processes the image in **A**. This operation—the convolution of the image in **A** with the profile in **B**—subtracts from each point in the visual field the average intensity in a large surrounding region. The neural representation of the object has largely lost the effects of shading, and the two tiles in question do indeed have different brightness values in this representation.

be proportional to the background intensity, a relationship known as *Weber’s law of adaptation*, which we encountered in considering somatic receptor sensitivity (Chapter 17). The visual system follows Weber’s law approximately: Over the entire range of vision, sensitivity decreases somewhat less steeply with increasing background intensity (Figure 22-19B).

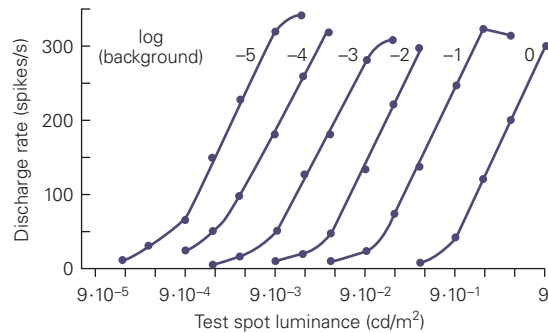
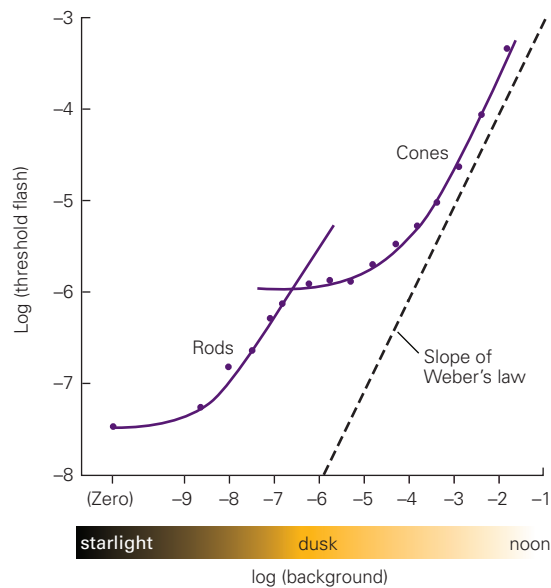
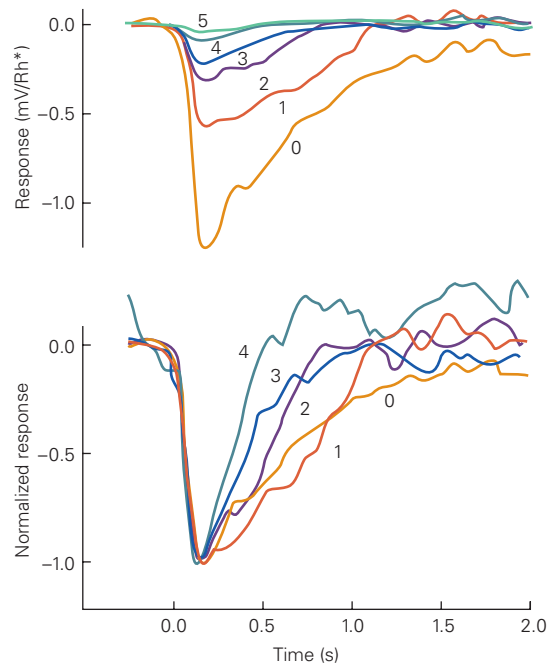
Multiple Gain Controls Occur Within the Retina

The enormous change in gain required for light adaptation arises at multiple sites within the retina. In starlight, a single rod cell is stimulated by a photon only every few seconds, a rate insufficient to alter the cell’s adaptation status. However, a retinal ganglion cell combines signals from many rods, thus receiving a steady stream of photon signals that can elicit a light-dependent gain change in the cell.

At somewhat higher light intensities, a rod bipolar cell begins to adapt, changing its responsiveness depending on the average light level. Next, we reach a light intensity at which the gain of individual rod cells gradually decreases. Beyond that, the rods saturate: All their cGMP-dependent channels are closed,

and the membrane potential no longer responds to the light stimulus. By this time, around dawn, the much less sensitive cone cells are being stimulated effectively and gradually take over from the rods. As the ambient light increases further, toward noon, light adaptation results principally from gain changes within the cones.

The cellular mechanisms of light adaptation are best understood in the photoreceptors. The calcium-dependent feedback pathways discussed earlier have a prominent role. Recall that when a light flash closes the cGMP-gated channels, the resulting decrease in intracellular Ca^{2+} accelerates several biochemical reactions that terminate the response to the flash (see Figure 22-7B). When illumination is continuous, however, the Ca^{2+} concentration remains low, and all these reactions are therefore in a steady state that both lowers the gain and accelerates the time course of the receptor’s response to light (Figure 22-19C). As a result, the light-adapted photoreceptor can respond to rapid changes in intensity much more quickly. This has important consequences for human visual perception; the contrast sensitivity to high-frequency flicker increases with intensity, an effect observed in primate retinal ganglion cells as well (see Figure 22-14).

A Cat ganglion cell**B** Human subjects**C** Macaque rod cell**Figure 22–19** Light adaptation.

A. The receptive field of a cat retinal ganglion cell was illuminated uniformly at a steady background intensity, and a test spot was flashed briefly on the receptive field center. The peak firing rate following the flash was measured and plotted against the logarithm of the flash intensity. Each curve corresponds to a different background intensity, increasing by factors of 10 from left to right. (Reproduced, with permission, from Sakmann and Creutzfeldt 1969. Copyright © 1969 Springer.)

B. A small test spot was flashed briefly on a steadily illuminated background, and the flash intensity gradually increased to where a human subject could just detect it. The procedure was repeated at different background intensities. Here, the threshold flash intensity is plotted against the background intensity. The curve has two branches connected by a distinct kink: These correspond to the regimes of rod and cone vision. The slope

of Weber's law represents the idealization when the threshold intensity is proportional to the background intensity. (Adapted from Wyszecki and Stiles 1982.)

C. The top plot shows the responses of a macaque monkey's rod cell to flashes presented at varying background intensities. The cell's single-photon response was calculated from the recorded membrane potential divided by the number of rhodopsins (Rh) activated by the flash. The gain of the single-photon response decreases substantially with increasing background intensity. The background intensity, in $\text{photon}/\mu\text{m}^2/\text{s}$, is 0 for trace 0, 3.1 for trace 1, 12 for trace 2, 41 for trace 3, 84 for trace 4, and 162 for trace 5. In the bottom plot, the same data (except for the smallest response) are normalized to the same amplitude, showing that the time course of the single-photon response accelerates at high intensity. (Reproduced, with permission, from Schneeweis and Schnapf 2000.)

Light Adaptation Alters Spatial Processing

In addition to the sensitivity and speed of the retinal response, light adaptation also changes the rules of spatial processing. In bright light, many ganglion cells have a sharp center-surround structure in their receptive fields (see Figure 22–10). As the light dims, the antagonistic surround becomes broad and weak and eventually disappears. Under these conditions, the circuits of the retina function to simply accumulate the rare photons rather than computing local intensity gradients. These changes in receptive-field properties occur because of changes in the lateral inhibition produced by the networks of horizontal and amacrine cells (see Figure 22–3). An important regulator of these processes is dopamine, released in a light-dependent manner by specialized amacrine cells.

These retinal effects leave their signature on human perception. In bright light, our visual system prefers fine gratings to coarse gratings. But in dim light, we are most sensitive to coarse gratings: With the loss of center-surround antagonism, the low spatial frequencies are no longer attenuated (see Box 22–1 and Figure 22–13).

In conclusion, light adaptation has two important roles. One is to discard information about the intensity of ambient light while retaining information about object reflectances. The other is to match the small dynamic range of firing in retinal ganglion cells to the large range of light intensities in the environment. These large gain changes must be accomplished with graded neuronal signals before action potentials are produced in optic nerve fibers, because the firing rates of these fibers can vary effectively over only two orders of magnitude. In fact, the crucial need for light adaptation may be why this neural circuitry resides in the eye and not in the brain at the other end of the optic nerve.

Highlights

1. The retina transforms light patterns projected onto photoreceptors into neural signals that are conveyed through the optic nerve to specialized visual centers in the brain. Different populations of ganglion cells transmit multiple neural representations of the retinal image along parallel pathways.
2. The retina discards much of the stimulus information available at the receptor level and extracts certain low-level features of the visual field useful to the central visual system. Fine spatial resolution is maintained only in a narrow region at the center of gaze. Intensity gradients in the image, such as

object edges, are emphasized over spatially uniform portions; temporal changes are enhanced over unchanging parts of the scene.

3. The retina adapts flexibly to the changing conditions for vision, especially the large diurnal changes in illumination. Information about the absolute light level is largely discarded, favoring the subsequent analysis of object reflectances within the scene.
4. The transduction of light stimuli begins in the outer segment of the photoreceptor cell when a pigment molecule absorbs a photon. This sets in motion an amplifying G protein cascade that ultimately reduces the membrane conductance, hyperpolarizes the photoreceptor, and decreases glutamate release at the synapse. Multiple feedback mechanisms, in which intracellular Ca^{2+} has an important role, serve to turn off the enzymes in the cascade and terminate the light response.
5. Rod photoreceptors are efficient collectors of light and serve nocturnal vision. Cones are much less sensitive and function throughout the day. Cones synapse onto bipolar cells that in turn excite ganglion cells. Rods connect to specialized rod bipolar cells whose signals are conveyed through amacrine cells to the cone bipolar cells.
6. The vertical excitatory pathways are modulated by horizontal connections that are primarily inhibitory. Through these lateral networks, light in the receptive-field surround of a ganglion cell counteracts the effect of light in the center. The same negative-feedback circuits also sharpen the transient response of ganglion cells.
7. The segregation of information into parallel pathways and the shaping of response properties by inhibitory lateral connections are pervasive organizational principles in the visual system.

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Intermediate-Level Visual Processing and Visual Primitives

Internal Models of Object Geometry Help the Brain Analyze Shapes

Depth Perception Helps Segregate Objects From Background

Local Movement Cues Define Object Trajectory and Shape

Context Determines the Perception of Visual Stimuli

Brightness and Color Perception Depend on Context

Receptive-Field Properties Depend on Context

Cortical Connections, Functional Architecture, and Perception Are Intimately Related

Perceptual Learning Requires Plasticity in Cortical Connections

Visual Search Relies on the Cortical Representation of Visual Attributes and Shapes

Cognitive Processes Influence Visual Perception

Highlights

WE HAVE SEEN IN Chapters 21 and 22 that the eye is not a mere camera, but instead contains sophisticated retinal circuitry that decomposes the retinal image into signals representing contrast and movement. These data are conveyed through the optic nerve to the primary visual cortex, which uses this information to analyze the shape of objects. It first identifies the boundaries of objects, represented by numerous short line segments, each with a specific orientation. The cortex then integrates this information into a representation of specific objects, a process referred to as *contour integration*.

These two steps, local analysis of orientation and contour integration, exemplify two distinct stages of visual processing. Computation of local orientation is an example of low-level visual processing, which is concerned with identifying local elements of the light structure of the visual field. Contour integration is an example of intermediate-level visual processing, the first step in generating a representation of the unified visual field. At the earliest stages of analysis in the cerebral cortex, these two levels of processing are accomplished together.

A visual scene comprises many thousands of line segments and surfaces. Intermediate-level visual processing is concerned with determining which boundaries and surfaces belong to specific objects and which are part of the background (see Figure 21–4). It is also involved in distinguishing the brightness and color of a surface from the intensity and wavelength of light reflected from that surface. The physical characteristics of reflected light result as much from the intensity and color balance of the light that illuminates a surface as from the color of that surface. Determining the actual surface color of a single object requires comparison of the wavelengths of light reflected from multiple surfaces in a scene.

Intermediate-level visual processing thus involves assembling local elements of an image into a unified percept of objects and background. Although determining which elements belong together in a single object is a highly complex problem with an astronomical number of potential solutions, each relay in the visual circuitry of the brain has built-in logic that

allows assumptions to be made about the likely spatial relationships between elements. In certain cases, these inherent rules can lead to the illusion of contours and surfaces that do not actually exist in the visual field (Figure 23–1).

Three features of visual processing help overcome ambiguity in the signals from the retina. First, the way in which a visual feature is perceived depends on everything that surrounds it. The perception of a point, line, or surface, for example, depends on the relationship between that feature and what else is present in the scene. That is, the response of a neuron in the

visual cortex is context-dependent: It depends as much on the presence of contours and surfaces outside the cell's receptive field as on the attributes within it. Second, the functional properties of neurons in the visual cortex can be altered by visual experience or perceptual learning. Finally, visual processing in the cortex is subject to the influence of cognitive functions, specifically attention, expectation, and “perceptual task” (the active engagement in visual discrimination or detection). The interaction between these three factors—the context or entire set of signals representing a scene, experience-dependent changes in cortical circuitry,

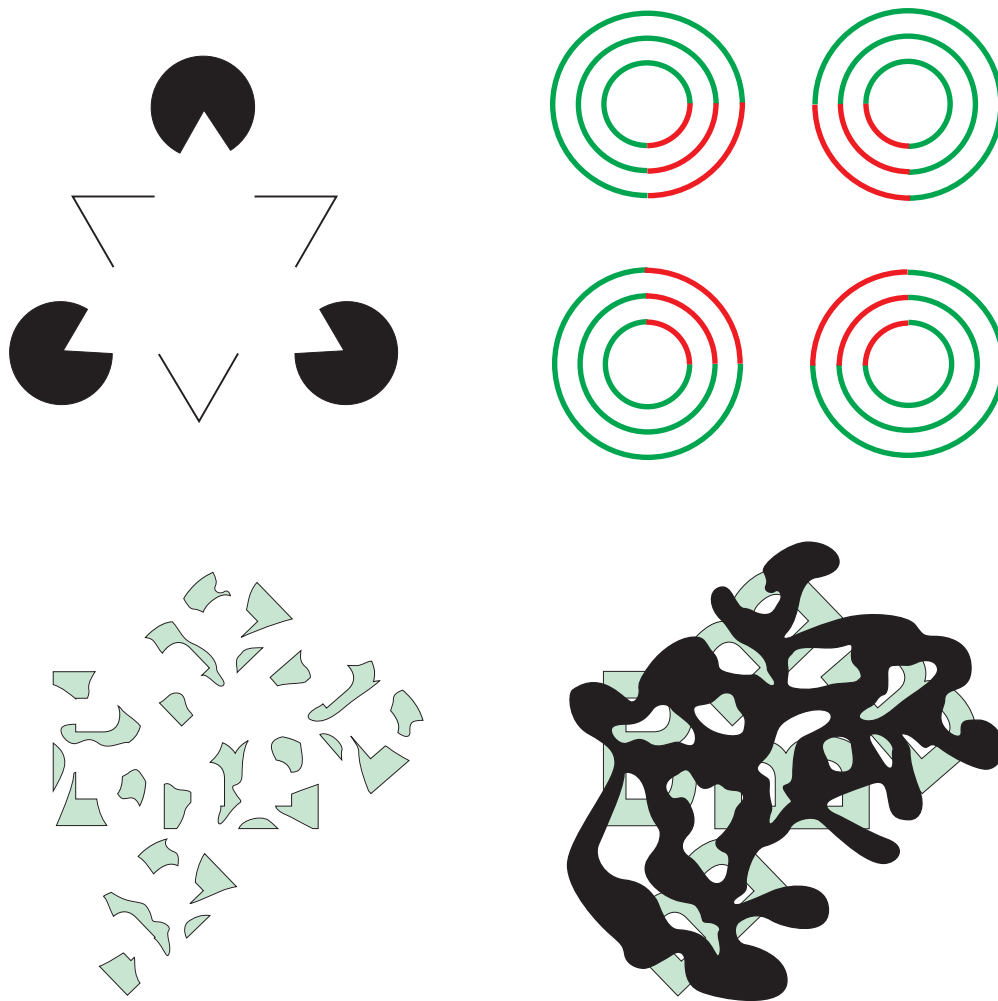


Figure 23–1 Illusory contours and perceptual fill-in. The visual system uses information about local orientation and contrast to construct the contours and surfaces of objects. This constructive process can lead to the perception of contours and surfaces that do not appear in the visual field, including those seen in illusory figures. **Top left:** In the Kanizsa triangle illusion, one perceives continuous boundaries extending between the apices of a white triangle, even though the only real contour elements are

those formed by the Pac-Man-like figures and the acute angles. **Top right:** The inside and outside of the illusory pink square are the same white color as the page, but a continuous transparent pink surface within the square is perceived. **Bottom:** Occluding surfaces can also facilitate contour integration and surface segmentation. The irregular shapes on the left appear to be unrelated, but when they are partially occluded by black shapes (right), they are easily seen as fragments of the letter B.

and expectation—is vital to the visual system’s analysis of complex scenes.

In this chapter, we examine how the brain’s analysis of the local features in a visual scene, or *visual primitives*, proceeds in parallel with the analysis of more global features. Visual primitives include contrast, line orientation, brightness, color, movement, and depth. Each type of visual primitive is subject to the integrative action of intermediate-level processing. Lines with particular orientations are integrated into object contours, local contrast information into surface brightness and surface segmentation, wavelength selectivity into color constancy, and directional selectivity into object motion.

The analysis of visual primitives begins in the retina with the detection of brightness and color and continues in the primary visual cortex with the analysis of orientation, direction of movement, and stereoscopic depth. Properties related to intermediate-level visual processing are analyzed together with visual primitives in the visual cortex starting in the primary visual cortex (V1), which plays a role in contour integration and surface segmentation. Other areas of the visual cortex specialize in different aspects of this task: V2 analyzes properties related to object surfaces, V4 integrates information about color and object shape, and V5—the middle temporal area or MT—integrates motion signals across space (Figure 23–2).

Internal Models of Object Geometry Help the Brain Analyze Shapes

A first step in determining an object’s contour is identification of the orientation of local parts of the contour. This step commences in V1, which plays a critical role in both local and global analysis of form.

Neurons in the visual cortex respond selectively to specific local features of the visual field, including orientation, binocular disparity or depth, and direction of movement, as well as to properties already analyzed in the retina and lateral geniculate nucleus, such as contrast and color. Orientation selectivity, the first emergent property identified in the receptive fields of cortical neurons, was discovered by David Hubel and Torsten Wiesel in 1959.

Neurons in both the retina (Chapter 22) and the lateral geniculate nucleus (Chapter 21) have circular receptive fields with a center-surround organization. They respond to the light–dark contrasts of edges or lines in the visual field but are not selective for the orientations of those edges (see Figure 21–9). In the visual cortex, however, neurons respond selectively to lines of particular orientations. Each neuron responds to a narrow range of orientations, approximately 40°, and different neurons respond optimally to distinct orientations. Hubel and Wiesel proposed that this orientation selectivity reflects the arrangement of the inputs

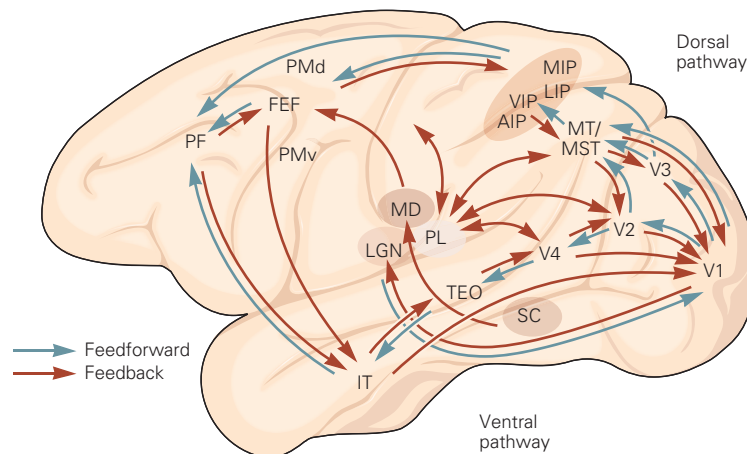


Figure 23–2 Cortical areas involved with intermediate-level visual processing. Many cortical areas in the macaque monkey, including V1, V2, V3, V4, and middle temporal area (MT), are involved with integrating local cues to construct contours and surfaces and segregating foreground from background. The shaded areas extend into the frontal and temporal lobes because cognitive output from these areas, including attention, expectation, and behavioral task, contributes to the process of scene segmentation. (Abbreviations: AIP, anterior intraparietal

cortex; FEF, frontal eye fields; IT, inferior temporal cortex; LGN, lateral geniculate nucleus; LIP, lateral intraparietal cortex; MD, medial dorsal nucleus of thalamus; MIP, medial intraparietal cortex; MST, medial superior temporal cortex; MT, middle temporal cortex; PF, prefrontal cortex; PL, pulvinar; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; SC, superior colliculus; TEO, occipitotemporal cortex; VIP, ventral intraparietal cortex; V1, V2, V3, V4, primary, secondary, third, and fourth visual areas.)

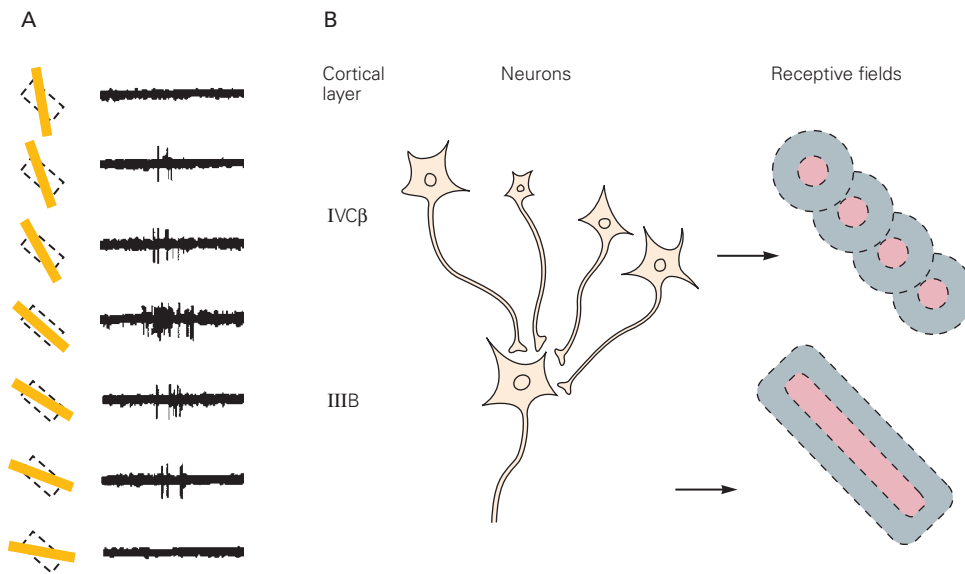


Figure 23-3 Orientation selectivity and mechanisms.

A. A neuron in the primary visual cortex responds selectively to line segments that fit the orientation of its receptive field. This selectivity is the first step in the brain's analysis of an object's form. (Reproduced, with permission, from Hubel and Wiesel 1968. Copyright © 1968 The Physiological Society.)

B. The orientation of the receptive field is thought to result from the alignment of the circular center-surround receptive fields of several presynaptic cells in the lateral geniculate nucleus. In the monkey, individual neurons in layer IVCβ of V1 have unoriented receptive fields. However, when several neighboring IVCβ cells project to a neuron in layer IIIB they create a receptive field with a specific orientation for that postsynaptic cell.

from the lateral geniculate nucleus, and there is now a body of supportive evidence for the idea. Each V1 neuron receives input from several neighboring geniculate neurons whose center-surround receptive fields are aligned so as to represent a particular axis of orientation (Figure 23-3). Two principal types of orientation-selective neurons, simple and complex, have been identified.

Simple cells have receptive fields divided into ON and OFF subregions (Figure 23-4). When a visual stimulus such as a bar of light enters the receptive field's ON subregion, the neuron fires; the cell also responds when the bar leaves the OFF subregion. Simple cells have a characteristic response to a moving bar; they discharge briskly when a bar of light leaves an OFF region and enters an ON region. The responses of these cells are therefore highly selective for the position of a line or edge in space.

Complex cells are less selective for the position of object boundaries. They lack discrete ON and OFF subregions (Figure 23-4) and respond similarly to light and dark at all locations across their receptive fields. They fire continuously as a line or edge stimulus traverses their receptive fields. Hubel and Wiesel proposed that the complex cells are a second stage of the elaboration of receptive fields after simple receptive fields and are built by overlapping simple receptive fields.

As one considers the range of receptive field properties that have been described in the early visual cortical areas, it is important to point out phylogenetic differences, with different species differing in the location in which these properties are first expressed and in the kinds of properties that are represented. In the cat, the target layer of the visual cortex for lateral geniculate neurons has oriented simple cells; it had been presumed that these cortical cells represent an obligatory first stage in the cortical processing of visual information, between the center-surround circularly symmetric receptive fields in the lateral geniculate nucleus and the receptive fields of complex cells in the superficial cortical layers. In primates, however, the geniculate target layers, 4Cα and β, have circularly symmetric, unoriented receptive fields. The postsynaptic target of the layer 4C cells, predominantly the superficial layers of the cortex, is populated with complex cells, therefore skipping a simple cell stage. In the mouse, orientation selectivity is seen in the lateral geniculate nucleus. The preceding comparison points out a few characteristics of the evolution of visual processing. One is the encephalization of function, where properties such as orientation are shifted to later stages of processing over stages of evolution. Another is the development of new pathways. It has been suggested that the