

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

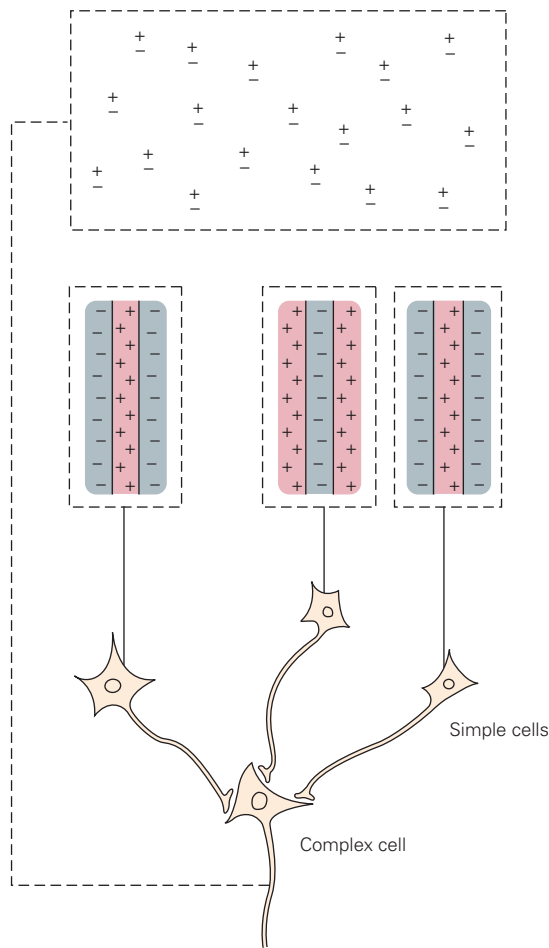


Figure 23-4 Simple and complex cells in the visual cortex. The receptive fields of simple cells are divided into subfields with opposite response properties. In an ON subfield (indicated by +), the onset of a light triggers a response in the neuron; in an OFF subfield (indicated by -), the extinction of a bar of light triggers a response. Complex cells have overlapping ON and OFF regions and respond continuously as a line or edge traverses the receptive field along an axis perpendicular to the receptive-field orientation.

magnocellular pathway in the monkey is equivalent to the entire geniculostriate pathway in the cat, whereas the parvocellular pathway, which mediates higher-resolution vision and color vision, is new to the primate.

Moving stimuli are often used to study the receptive fields of visual cortex neurons, not only to simulate the conditions under which an object moving in space is detected but also to simulate the conditions produced by eye movements. As we scan the visual environment, the boundaries of stationary objects move across the retina. In fact, visual perception requires eye movement. Visual cortex neurons do not respond to an image that is stabilized on the retina. These neurons

require transient stimulation (moving or flashing stimuli) in order to be activated.

Some visual cortex neurons have receptive fields in which an excitatory center is flanked by inhibitory regions. Inhibitory regions along the axis of orientation, a property known as *end-inhibition*, restrict a neuron's responses to lines of a certain length (Figure 23-5). End-inhibited neurons respond well to a line that does not extend into the inhibitory flanks but lies entirely within the excitatory part of the receptive field. Because the inhibitory regions share the orientation preference of the central excitatory region, end-inhibited cells are selective for line curvature and also respond well to corners.

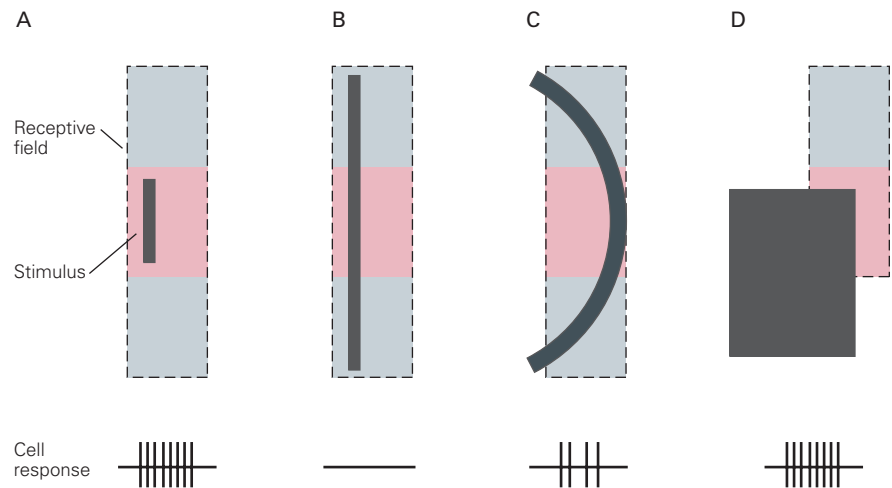
To define the shape of the object as a whole, the visual system must integrate the information on local orientation and curvature into object contours. The way in which the visual system integrates contours reflects the geometrical relationships present in the natural world (Figure 23-6). As originally pointed out by Gestalt psychologists early in the 20th century, contours that are immediately recognizable tend to follow the rule of good continuation (curved lines maintain a constant radius of curvature and straight lines stay straight). In a complex visual scene, such smooth contours tend to "pop out," whereas more jagged contours are difficult to detect.

The responses of a visual cortex neuron can be modulated by stimuli that themselves do not activate the cell and therefore lie outside the receptive field's core. This *contextual modulation* endows a neuron with selectivity for more complex stimuli than would be predicted by placing the components of a stimulus at different positions in and around the receptive field. The same visual features that facilitate the detection of an object in a complex scene (Figure 23-6A) also apply to contextual modulation. The properties of the features that confer perception of contours, even illusory ones, are reflected in the responses of neurons in the primary visual cortex, which are sensitive to the global characteristics of contours, even those that extend well outside their receptive fields.

Contextual influences over large regions of visual space are likely to be mediated by connections between multiple columns of neurons in the visual cortex that have similar orientation selectivity (Figure 23-6B). These connections are formed by pyramidal-cell axons that run parallel to the cortical surface (see Figure 21-16). The extent and orientation dependency of these horizontal connections provide the interactions that could mediate contour saliency (see Figure 21-14).

Central to the process of contour integration is the idea of the association field. The association field refers

Figure 23-5 End-inhibited receptive fields. Some receptive fields have a central excitatory region flanked by inhibitory regions that have the same orientation selectivity. Thus, a short line segment or a long curved line will activate the neuron (A and C), but a long straight line will not (B). A neuron with a receptive field that displays only one inhibitory region in addition to the excitatory region can signal the presence of corners (D).



to the interactions across visual space required to perceptually link contour elements into global contours. It underlies the Gestalt principle of good continuation and the perceptual saliency of smooth contours embedded in complex scenes. Physiologically, it underlies the facilitation of neuronal responses by contour elements extending outside their “classical” receptive fields. Anatomically, it is mediated in part by the relationship between long-range horizontal connections and cortical functional architecture. Though it has been investigated most extensively in primary visual cortex, because of the ubiquity of horizontal connections across all areas of cortex, it is likely to be a strategy for associating bits of information that are mapped within every cortical area. The functional role of the association field in cortical areas outside of V1 depends on how information is mapped across the cortical surface and the relationship between these maps and the plexus of horizontal connections.

Depth Perception Helps Segregate Objects From Background

Depth is another key feature in determining the perceived shape of an object. An important cue for the perception of depth is the difference between the two eyes’ views of the world, which must be computed and reconciled by the brain. The integration of binocular input begins in the primary visual cortex, the first level at which individual neurons receive signals from both eyes. The balance of input from the two eyes, a property known as ocular dominance, varies among cells in V1.

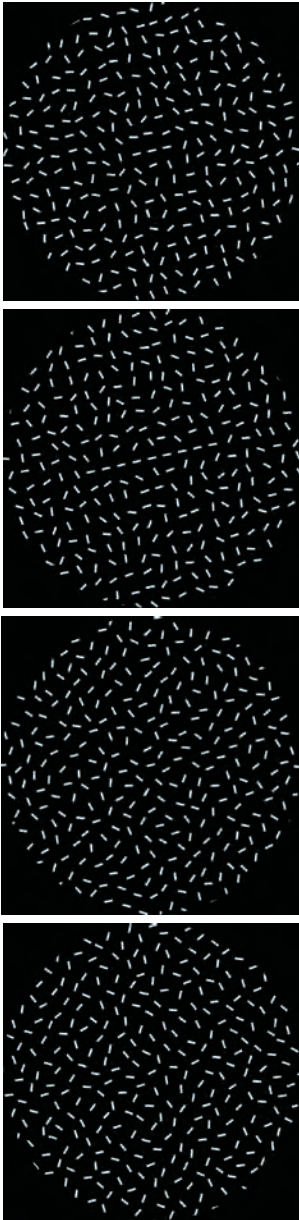
Binocular neurons in many visual cortical areas are also selective for depth, which is computed from

the relative retinal positions of objects placed at different distances from the observer. An object that lies in the *plane of fixation* produces images at corresponding positions on the two retinas (Figure 23-7). The images of objects that lie in front of or behind the plane of fixation fall on slightly different locations in the two eyes, a property known as binocular disparity. Individual neurons can be selective for a narrow range of disparities and therefore positions in depth. Some are selective for objects lying on the plane of fixation (tuned excitatory or inhibitory cells), whereas others respond only when objects lie in front of the plane of fixation (near cells) or behind that plane (far cells).

Depth plays an important role in the perception of object shape, in surface segmentation, and in establishing the three-dimensional properties of a scene. Objects that are placed near an observer can partially occlude those situated farther away. A surface passing behind an object is perceived as continuous even though its two-dimensional image on each retina represents two surfaces separated by the occluder. When the brain encounters a surface interrupted by gaps that have appropriate alignment and contrast, and lying in the near-depth plane, it fills in the gaps to create a continuous surface (Figure 23-8).

Although the depth of a single object can be established easily, determining the depths of multiple objects within a scene is a much more complex problem that requires linking the retinal images of all objects in the two eyes. The disparity calculation is therefore a global one: The calculation in one part of the visual image influences the calculation for other parts. When the assignment of depth is unambiguous in one part of an image, that information is applied to other parts of the image where there is insufficient information to

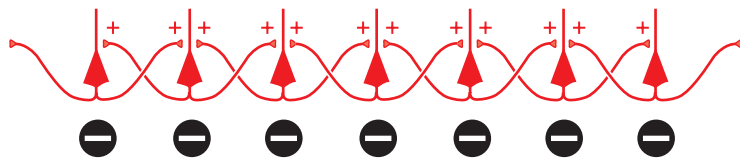
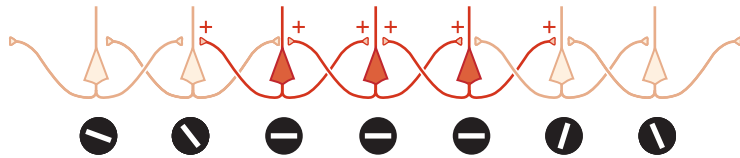
A Visual field



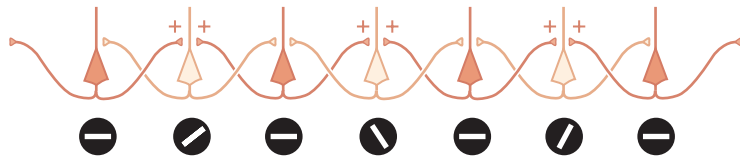
B Laterally connected V1 neurons

Features affecting contour saliency

Number of line elements



Spacing of collinear line elements



Smoothness of contour

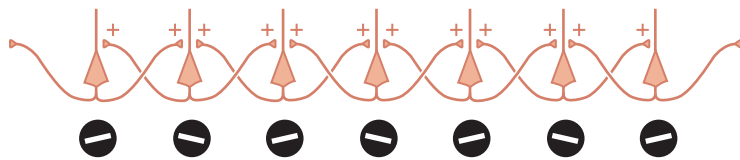


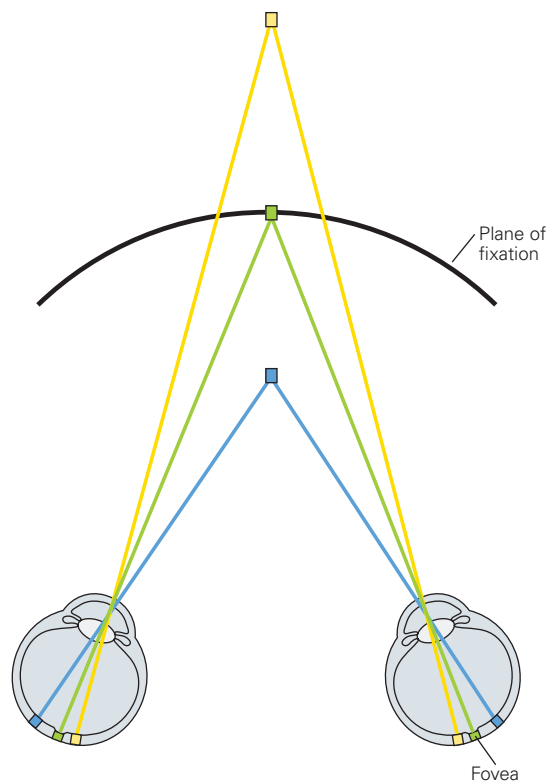
Figure 23–6 Contour integration reflects the perceptual rules of proximity and good continuation. (Adapted, with permission, from Li and Gilbert 2002.)

A. A straight line composed of one or more contour elements with the same oblique orientation appears in the center of each of the four images here. In some images, the line pops out more or less immediately, without searching. Factors that contribute to contour saliency include the number of contour elements (compare the first and second frames), the spacing of the elements (third frame), and the smoothness of the contour

(bottom frame). When the spacing between elements is too large or the orientation difference between them too great, one must search the image to find the contour.

B. These perceptual properties are reflected in the horizontal connections between columns of V1 neurons with similar orientation selectivity. As long as the visual elements are spaced sufficiently close together, excitation can propagate from cell to cell, thus facilitating the responses of V1 neurons. Each neuron in the network then augments the responses of neurons on either side, and the facilitated responses propagate across the network.

A Binocular disparity of retinal images

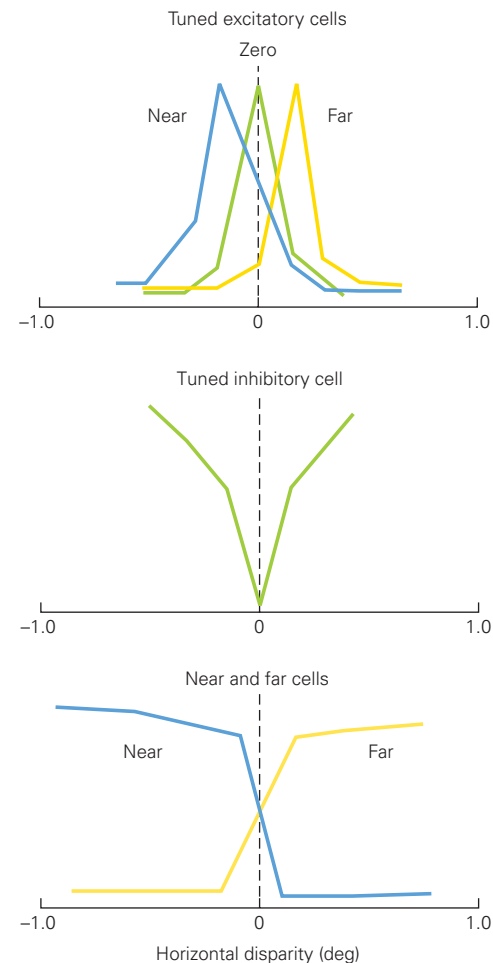
**Figure 23-7** Stereopsis and binocular disparity.

A. Depth is computed from the positions at which images occur in the two eyes. The image of an object lying in the plane of fixation (**green**) falls on corresponding points on the two retinas. Images of objects lying in front of the plane of fixation (**blue**) or behind it (**yellow**) fall on noncorresponding locations on the two retinas, a phenomenon termed *binocular disparity*.

determine depth, a phenomenon known as disparity capture.

Random-dot stereograms provide a dramatic demonstration of the global scope of disparity analysis. The visual information presented to each eye appears to be incoherent, but when the stereogram is viewed binocularly, the disparity between the random array of dots in the two images allows an embedded shape to become visible (Figure 23-8C). The calculation underlying this percept is not simple, but requires determining which

B Disparity-selective neurons



B. Neurons in many visual cortical areas are selective for particular ranges of disparity. Each plot shows the responses of a neuron to binocular stimuli with different disparities (abscissa). Some neurons are tuned to a narrow range of disparities and thus have particular disparity preferences (tuned excitatory or tuned inhibitory neurons), whereas others are tuned broadly for objects in front of the fixation plane (near cells) or beyond the plane (far cells). (Adapted, with permission, from Poggio 1995. Copyright © 1995 Oxford University Press.)

features shown to the left eye correspond to features seen by the right eye and propagating local disparity information across the image.

Neurons in area V2 display sensitivity to global disparity cues. Distant depth cues can be used to link contour elements that belong to an object, and to separate them from the object background (Figure 23-B).

In addition to binocular disparity, the visual system also uses many monocular cues to discriminate depth. Depth determination through monocular

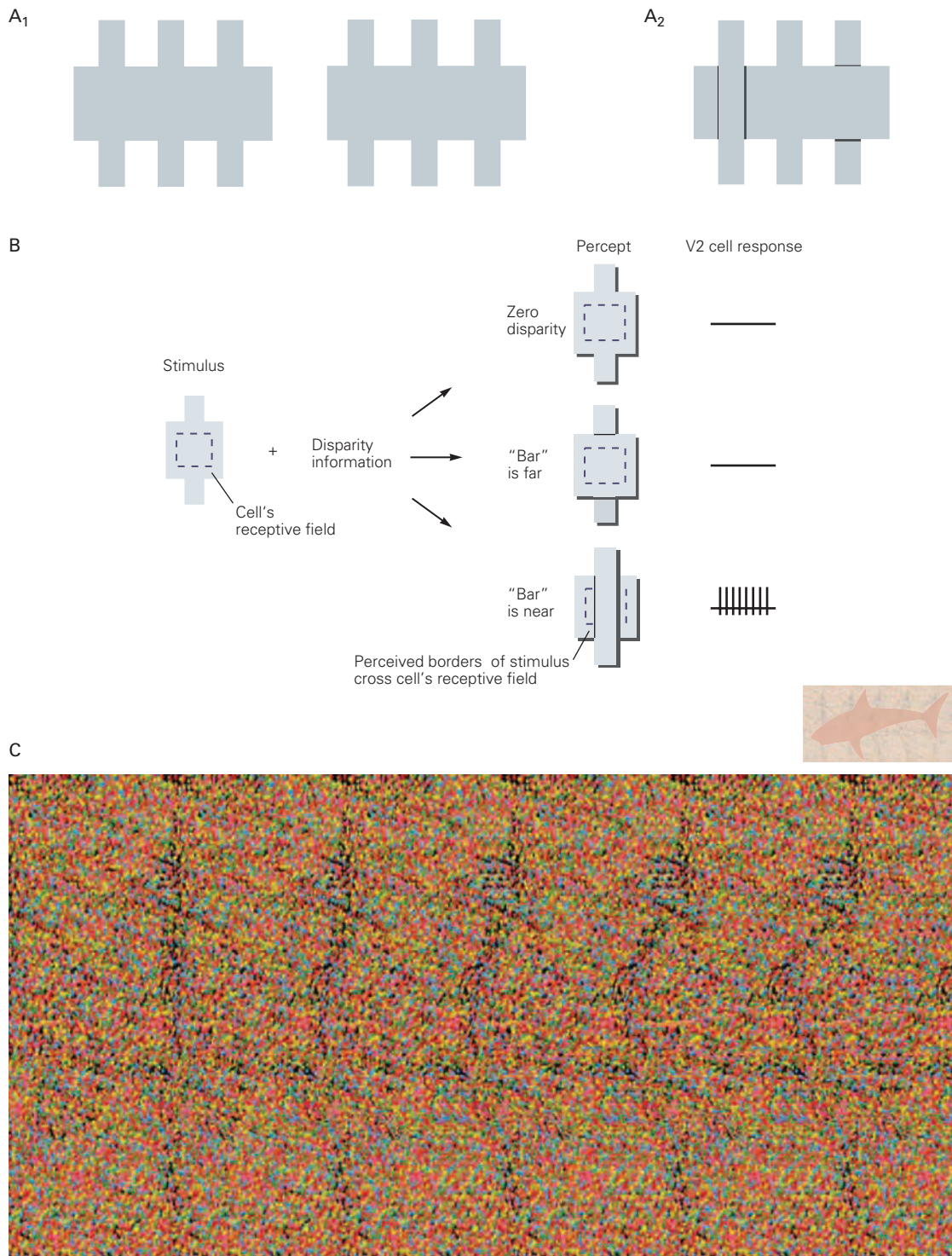


Figure 23-8 Global analysis of binocular disparity.

A. 1. Depth cues contribute to surface segmentation. If you view one of the images of three gray vertical bars crossing a gray horizontal rectangle, you see a uniform gray area within the rectangle. **2.** However, if you fuse the two rectangles with diverged eyes, the three vertical bars fall on the two retinas with near, zero, and far disparity. Seen this way, the bar at the left appears to hover in front of the rectangle with an illusory vertical edge crossing the rectangle, whereas the bar at the right appears to lie behind the edges of the horizontal rectangle.

B. A neuron in area V2 responds to illusory edges formed by binocular disparity cues. When the cell's receptive field

is centered in the gray square, the cell does not respond to a vertical bar that has far disparity or the same disparity as the square. When the vertical bar has near disparity, the cell responds as the illusory vertical edge crosses its receptive field. (Reproduced, with permission, from Bakin, Nakayama, and Gilbert 2000. Copyright © 2000 Society for Neuroscience.)

C. A random-dot stereogram is seen as a random array of colored dots until you diverge or converge your eyes to bring the adjacent dark vertical stripes into register, producing a three-dimensional image of a shark that emerges from the background. This effect stems from systematic disparity for selected sets of dots. (© Fred Hsu/Wikimedia Commons/CC-BY-SA-3.0.)

cues, such as size, perspective, occlusion, brightness, and movement, is not difficult. Another cue that originates outside the visual system is vergence, the angle between the optical axes of the two eyes for objects at varying distances. Yet another binocular cue, known as DaVinci stereopsis, is the presence of features visible to one eye but occluded in the other eye's view.

Neurons in areas V1 and V2 also signal foreground-background relationships. A cell with its receptive field in the center of a pattern within a larger surface may respond even when the boundary of that surface is distant from the receptive field. This response helps differentiate the object from its background. In making sense of an image, the brain must identify which edge belongs to which object and differentiate the edge of each object from the background. Some cells in area V2 have the property of "border ownership," firing only when a figure but not the background is to one side of the edge, even when the local edge information is identical in both instances (Figure 23–9).

Local Movement Cues Define Object Trajectory and Shape

The primary visual cortex determines the direction of movement of objects. Directional selectivity in neurons likely involves sequential activation of regions on different sides of the receptive field.

If an object moving at an appropriate velocity first encounters a region of a neuron's receptive field with long response latencies and then passes into regions with progressively shorter latencies, signals from throughout the receptive field will arrive at the cell simultaneously and the neuron will fire vigorously. If the object moves in the opposite direction, signals from the different regions will not summate and the cell may never reach the threshold for firing (Figure 23–10).

Early in the visual pathways, analysis of the movement of an object is limited by the size of the receptive fields of the sensory neurons. Even in the initial cortical areas V1 and V2, the receptive fields of neurons are small and might encompass only a fraction of an object. Eventually, however, information about the direction and speed of movement of discrete aspects of an object must be integrated into a computation of the movement of a whole object. This problem is more difficult than one might expect.

If one observes a complex shape moving through a small aperture, the part of the object's boundary

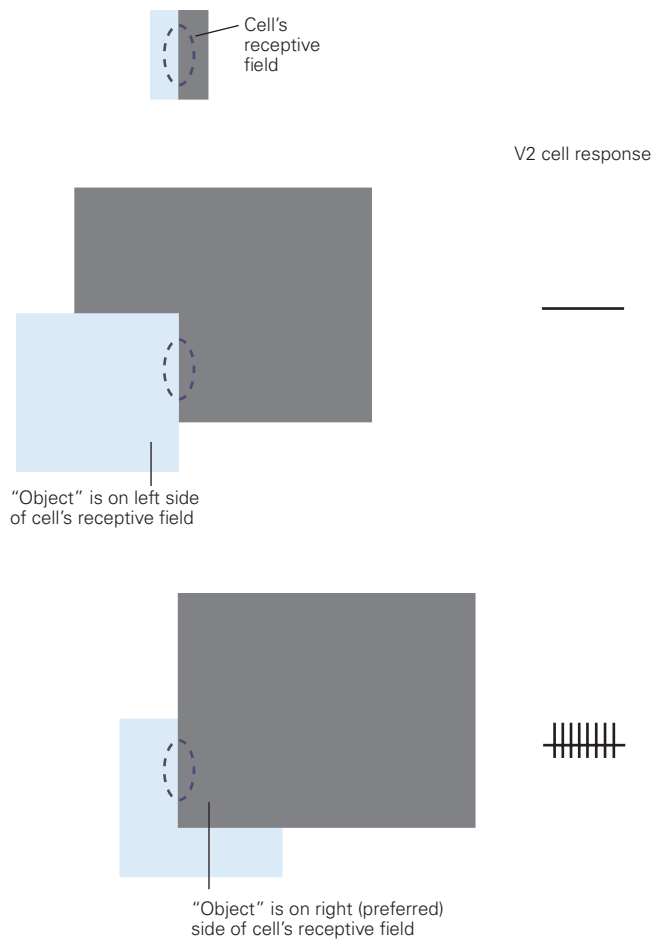


Figure 23–9 Border ownership. Cells in area V2 are sensitive to the boundaries of whole objects. Even though the local contrast is the same for the two rectangles within a cell's receptive field, the cell responds only when the boundary is part of the full rectangle that lies on the preferred side of the receptive field. (Adapted, with permission, from Zhou, Friedman, and von der Heydt 2000. Copyright © 2000 Society for Neuroscience.)

within the aperture appears to move in a direction perpendicular to the boundary's orientation (Figure 23–11A). One cannot detect a line's true direction of movement if the line's ends are not visible. The image of a line appears the same if it is moving slowly along an axis perpendicular to its orientation or more quickly along an oblique axis. This is the quandary presented by the receptive field of a V1 neuron. The visual system's solution is to assume that the movement of a contour is perpendicular to its orientation. Thus, an object is first presented to the visual system in countless small pieces with boundaries of different orientations, all of which appear to be moving in

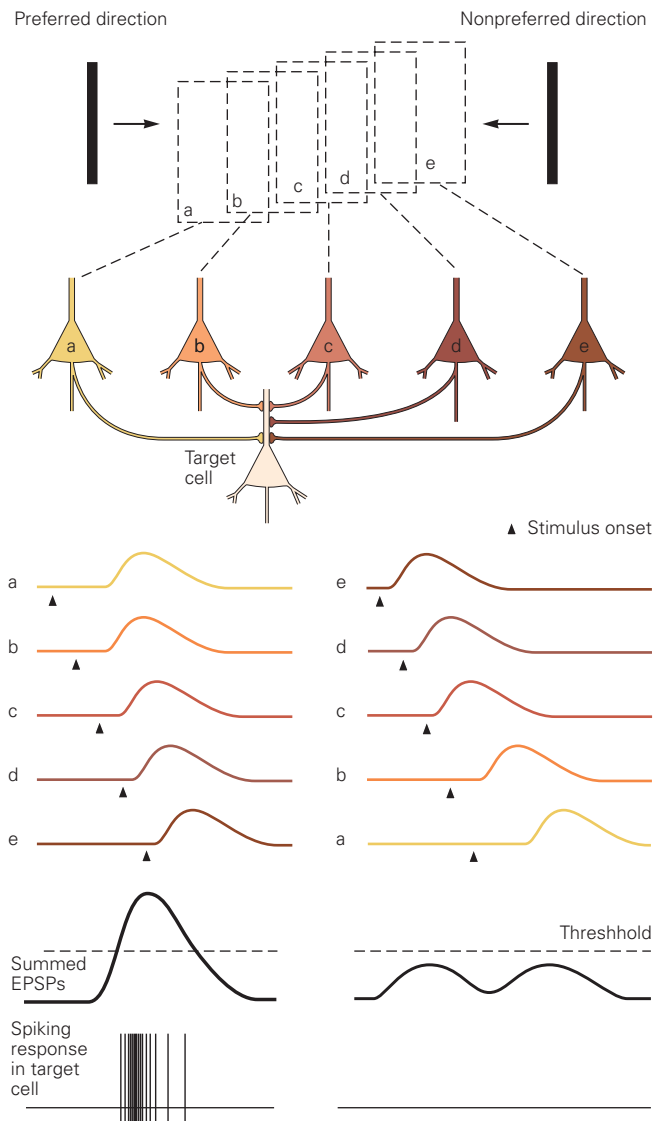


Figure 23-10 Directional selectivity of movement. A neuron's selectivity for direction of movement depends on the response latencies of presynaptic neurons relative to the onset of a stimulus. The response latencies of presynaptic neurons *a* and *b* are somewhat longer than those of neurons *d* and *e*. When a stimulus moves from left to right, neurons *a* and then *b* are activated first, but because their response latencies are longer, their inputs arrive at the target neuron superimposed with the inputs from neurons *d* and *e*, and the summated inputs cause the neuron to fire. In contrast, stimuli moving leftward produce signals that arrive in the target neuron at different times and therefore do not reach the cell's threshold for firing. (Abbreviation: EPSP, excitatory postsynaptic potential.) (Adapted, with permission, from Priebe and Ferster 2008. Copyright © 2008 Elsevier.)

different directions and at different velocities (Figure 23-11A).

Determining the direction of motion of an object requires resolving multiple cues. This can be demonstrated readily by placing one grating on top of another and moving the two in different directions. The resulting checkerboard pattern appears to move in an intermediate direction between the trajectories of the individual gratings (Figure 23-11B). This percept depends on the relative contrast of the gratings and the area of grating overlap. With large relative contrasts, the gratings appear to slide across each other, moving in their individual directions rather than together in a common direction.

An important determinant of perceived direction is scene segmentation, the separation of moving elements into foreground and background. In a scene with moving objects, segmentation is not based on local cues of direction; instead, perception of direction depends on scene segmentation. The barber-pole illusion provides another example of the predominance of global relationships over the perception of simple attributes. The rotating stripes are perceived as moving vertically along the long axis of the pole (Figure 23-11C). The perception of motion in the visual field uses a complex algorithm that integrates the bottom-up analysis of local motion signals with top-down scene segmentation.

Integration of local motion signals in monkeys has been observed in the middle temporal area (area MT or V5), an area specializing in motion. The neurons in this area are selective for a particular direction of movement of an overall pattern, rather than individual components of the pattern. This dependency on the overall pattern is also seen in the correspondence of their responses with the perceived direction in the barber-pole effect.

Context Determines the Perception of Visual Stimuli

Brightness and Color Perception Depend on Context

The visual system measures the surface characteristics of objects by comparing the light arriving from different parts of the visual field. As a result, the perception of brightness and color is highly dependent on context. In fact, perceived brightness and color can be quite different from what is expected from the physical properties of an object. At the same time, perceptual constancies make objects appear similar even when the brightness and wavelength distribution of the light

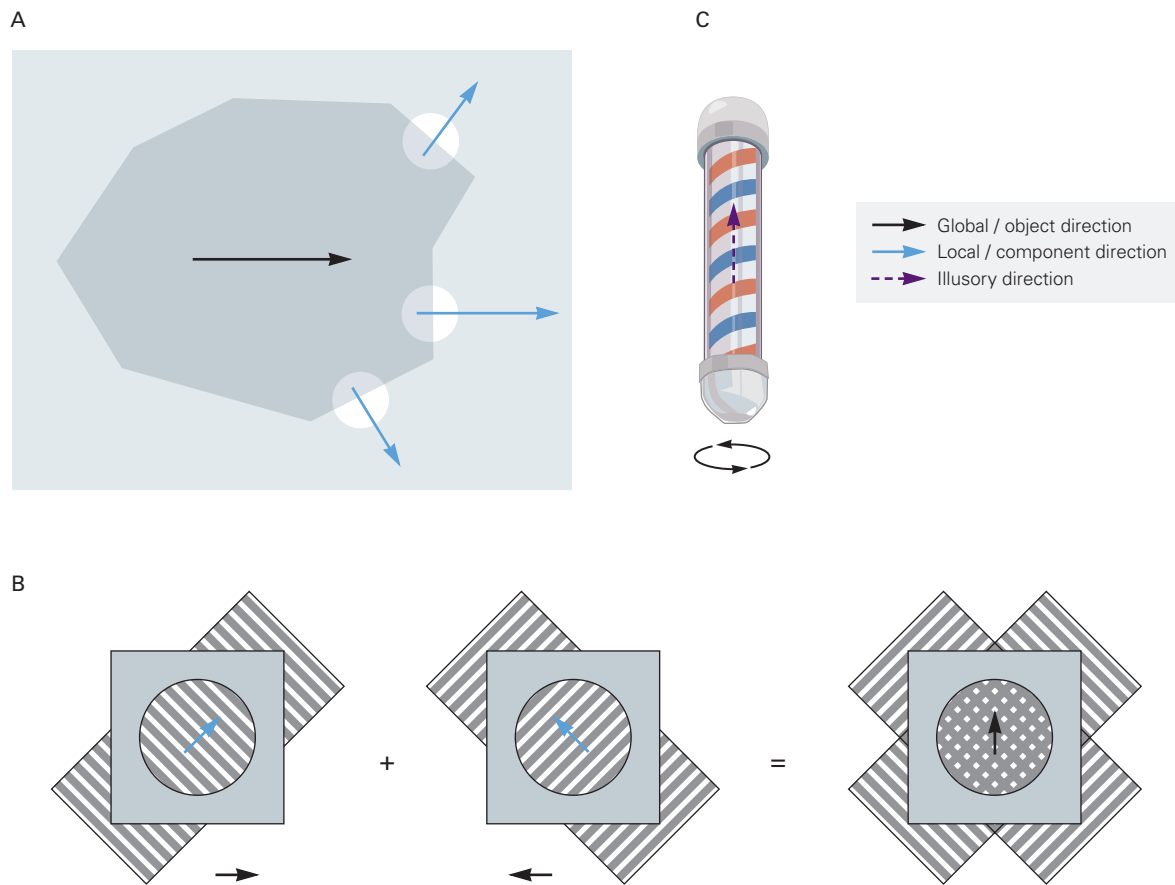


Figure 23-11 The aperture problem and barber-pole illusion.

A. Although an object moves in one direction, each component edge when viewed through a small aperture appears to move in a direction perpendicular to its orientation. The visual system must integrate such local motion signals into a unified percept of a moving object.

B. Gratings are used to test whether a neuron is sensitive to local or global motion signals. When the gratings are superimposed and moved independently in different directions, one

does not see the two gratings sliding past each other but rather a plaid pattern moving in a single, intermediate direction. Neurons in the middle temporal area of monkeys are responsive to such global motion rather than to local motion.

C. Motion perception is influenced by scene segmentation cues, as seen in the barber-pole illusion. Even though the pole rotates vertically, one perceives the stripes as moving horizontally, due to the global vertical rectangle surround of the barber pole enclosure.

that illuminates them changes from natural to artificial light, from sunlight to shadow, or from dawn to midday (Figure 23-12A).

As we move about or as the ambient illumination changes, the retinal image of an object—its size, shape, and brightness—also changes. Yet under most conditions, we do not perceive the object itself to be changing. As we move from a brightly lit garden into a dimly lit room, the intensity of light reaching the retina may vary a thousandfold. Both in the room's dim illumination and in the sun's glare, we nevertheless see a white shirt as white and a red tie as red. Likewise, as a friend walks toward you, she is seen as coming closer; you do not perceive her to be growing larger even though the

image on your retina does expand. Our ability to perceive an object's size and color as constant illustrates again a fundamental principle of the visual system: It does not record images passively, like a camera, but instead uses transient and variable stimulation of the retina to construct representations of a stable, three-dimensional world.

Another example of contextual influence is color induction, whereby the appearance of a color in one region shifts toward that in an adjoining region. Shape also plays an important role in the perception of surface brightness. Because the visual system assumes that illumination comes from above, gray patches on a folded surface appear very different when they lie on