2

Functional Organization of the Visual System

The visual system must convert the pattern of light that falls on the retina into perception. This involves a transformation of the visual image in several dimensions. Take, for example, depth perception: There are several cues to depth perception, including disparity, vergence, perspective, shading, texture gradients, interposition, motion parallax, size, and accommodation. For complete perception, all of these must be analyzed. Where some cues conflict with others (see Kaufman, 1974), the system must resolve the conflicts and come to a decision. Where the cues agree with each other, the system produces a perception of the distance of an object from the subject, its position in relation to other objects nearby, and the three-dimensional shape of the object.

As another example, consider color vision: The most important property of color, for the survival of the species, is not the pleasurable sensations that it gives, but the fact that it helps to recognize objects. The visual system has evolved so that the color of an object remains constant when lighted by different sources of illumination, and against different backgrounds. This is known as *object color constancy*. What the brain recognizes is a property of the object, namely the percentage of each wavelength that is reflected by the object (reflection spectrum). The composition of the wavelengths reaching the eye from the object is the product of the reflection spectrum and the illumination falling on the object—what the visual system does, as Helmholtz put it, is to "discount the source of illumination." This is a complicated calculation, as shown by numerous attempts in the last century to provide a mathematical formula for it.

One could provide a number of other examples, including shape perception, pattern perception, and control of eye movements, if space permitted. In all cases, the basic job of the visual system is to recognize objects and their position in space. Sometimes this leads to illusions such as the Ponzo illusion (Fig. 2.1). In this illusion the two cylinders are the same length, but the bottom one appears to be shorter because of the presence of the converging lines. However, this is not so much an illusion as the visual system

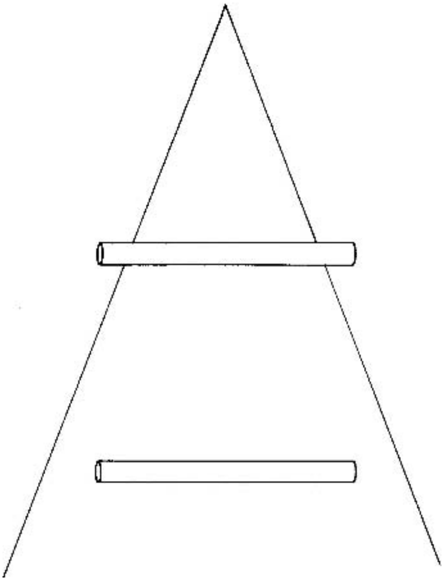

FIG. 2.1. Ponzo illusion. The two cylinders are the same length, but the converging lines make the top cylinder appear longer because of the effects of perspective.

operating in a sensible way to recognize distance. As another example, the brightness of an object, as well as its color, is influenced by the surroundings (Fig. 2.2). In this illustration, the ball on the top reflects the same amount of light as the ball on the bottom, but because the top one is seen against a dark background, it appears to be lighter than the bottom one. What this chapter is designed to do is to give a broad idea, to the extent that current knowledge permits, of how the visual system is organized to provide these constancies and perceptions.

1. General Anatomical Organization

The initial processing of the image takes place in the retina. The retina projects to four nuclei, with different functions: the lateral geniculate nucleus, for perception of objects; the superior colliculus, for control of eye movements; the pretectum, for control of the pupil; and the suprachiasmatic nucleus, for control of diurnal rhythms and hormonal changes (Fig. 2.3). In most of these areas, and in higher areas of the visual system, there is a topographic organization. That is, the retina maps to the nucleus in an organized fashion. Neighboring parts of the retina project to neighboring parts of the nucleus, so that there is a map of the field of view within the nucleus.

The lateral geniculate nucleus has several layers, and the two eyes project to separate layers. The lateral geniculate projects on to primary visual cortex (V1), which is also known as striate cortex because the input layer can be seen as a stripe without magnification. Primary visual cortex is where the signals from the two eyes come together. There are also projections to the cortex

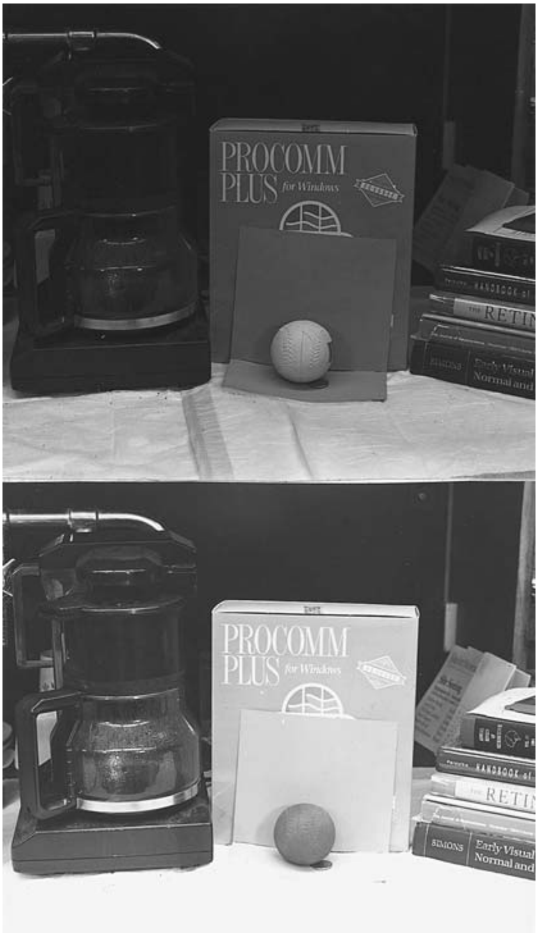

FIG. 2.2. How the brightness of an object depends on the background. Two photographs were taken of a scene with a light ball in the top scene and a dark ball in the bottom scene. Then the whole of the top scene was darkened, so that the amount of light coming from the two balls is identical. Because of contrast with the immediate background, the top ball looks lighter than the bottom one.

from the superior colliculus through the pulvinar, known as the extrastriate pathway to cortex.

Cortex in general has six layers (I, II, III, IV, V, and VI). Signals come in to layer IV. Layer IV projects to layers II and III, which send signals to other areas of cortex. Layers II and III project to layer V, which sends signals back to the superior colliculus. Layers II, III, and V project to layer VI, which sends signals back to the lateral geniculate nucleus. The complete story is far more complicated than this, but these are the predominant projections.

A large number of areas in the cerebral cortex deal with vision—at least 32 in the macaque monkey (Van Essen, Anderson, & Felleman, 1992) and 13 in the cat (Rosenquist, 1985). These have been best described in the monkey (Fig. 2.4). The large number of areas, and the even larger number of connections between them—305 at last count in the macaque—is bewildering. Broadly speaking, these areas can be thought of as lying along two pathways (Ungerleider & Pasternak, 2004). One goes through V1 and the secondary visual cortex (V2), then on to the temporal cortex. This pathway deals primarily

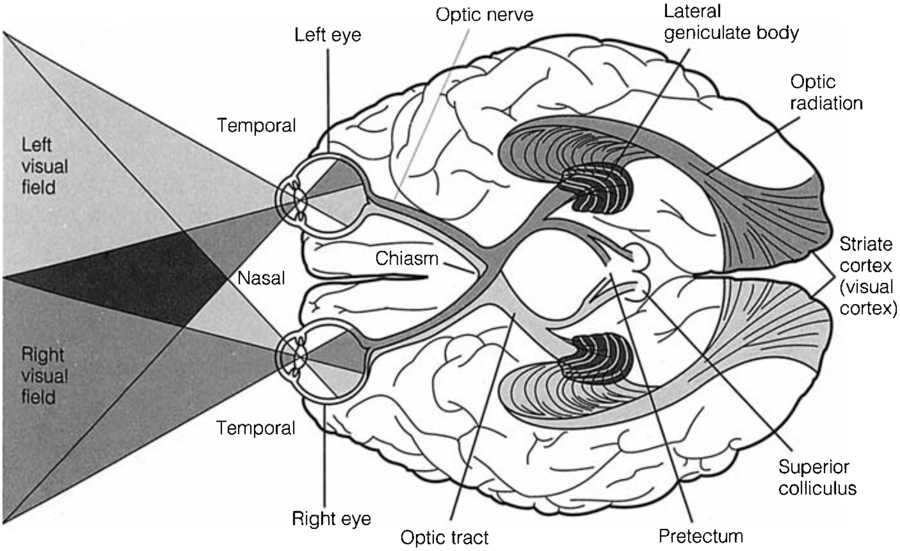

FIG. 2.3. Overall view of the visual system as seen from below. The retina projects to the lateral geniculate body, the superior colliculus, the pretectal area, and the suprachiasmatic nucleus (not shown). The lateral geniculate nucleus projects to the visual cortex. Axons from the nasal retina cross in the chiasm and axons from the temporal retina do not. Consequently, the left cortex deals with the right field of view and vice versa.

with what an object is, that is, its shape, form, and color. The other also goes through V1 and V2, and then on to the parietal cortex. This pathway deals primarily with where an object is and with the control of eye movements. In addition signals from different senses converge in the parietal pathway. Although the multiplicity of interconnections between areas in the parietal pathway and areas in the temporal pathway shows that this is an oversimplification, it is a useful one.

Different areas handle different properties of the visual stimulus. For example, V4 contains many cells that respond to color and shape, while V5 (also called MT) contains many cells that respond to movement (Zeki, 1978; Pasupathy & Connor, 2002). What specific properties are dealt with in the other 30 or so areas is currently a topic of active research. It will be many years before the differences between the various areas are completely characterized.

2. Function in the Retina

The main function of the retina is to convert information about brightness (speaking more correctly, luminance) into information about contrast (Kuffler, 1953). Generally speaking, the visual system is concerned with relative quantities—the luminance of an object in relation to the luminance of objects around it, the long wavelengths coming from an object in relation to medium and short wavelengths, and so on. Many of these relative comparisons are made in the retina. Just about the only function in the visual system

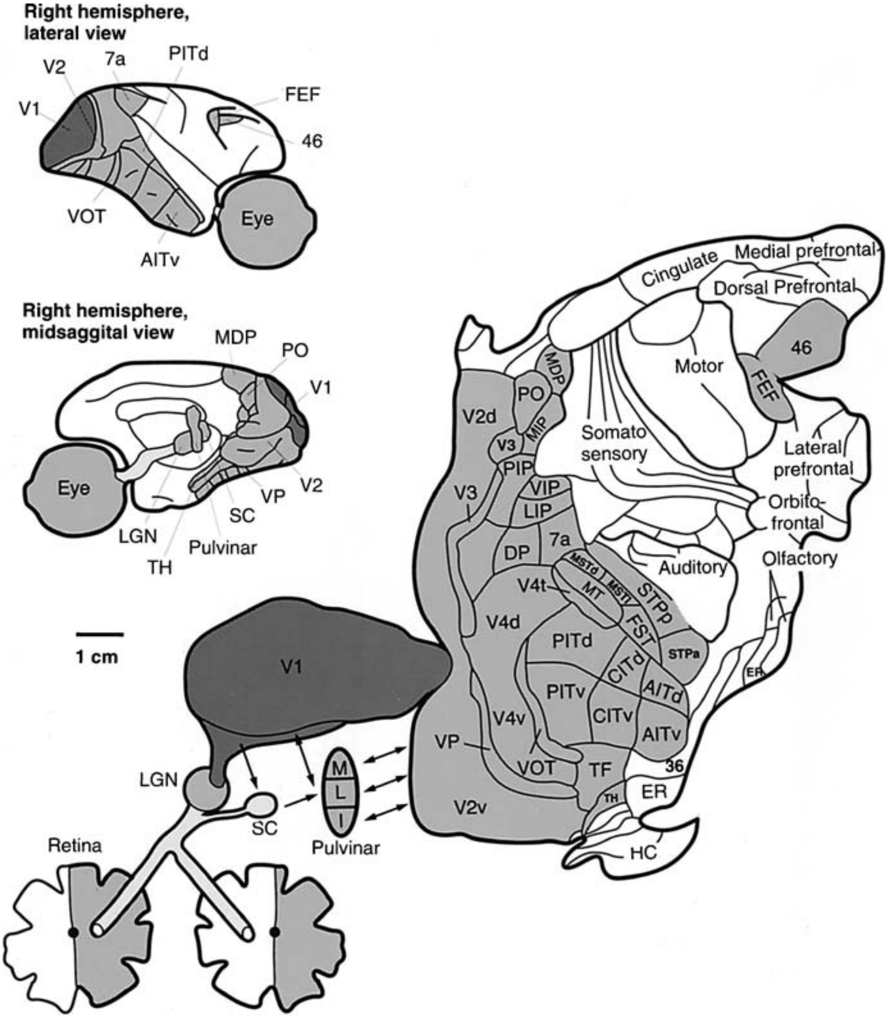

FIG. 2.4. An overview of the macaque visual system. On the left is a lateral view of the right cortex (top) and a midsaggital view looking at the medial surface with the left hemisphere removed (middle). Projections from the retina are summarized at the bottom: the geniculostriate pathway goes from the retina to the lateral geniculate nucleus (LGN) to V1; the extrastriate pathway goes from the retina to the superior colliculus (SC) to the pulvinar to V2 and other areas. On the right is shown a flattened view of the cortex with sulci and gyri smoothed out and with a cut between V1 and V2, which are in reality next to each other, to permit this illustration. Visual areas on the temporal pathway dealing with form and color are V4 and inferotemporal areas (PITd, PITv, CITd, CITv, AITd, AITv); visual areas on the parietal pathway dealing with location and eye movements are PO, VIP, LIP, and 7a; MT and MST, which deal with movement and disparity, feed into both of these pathways. MIP and VIP receive somatosensory as well as visual input. The function of many areas is not yet defined. [Reprinted with permission from Van Essen, D. C., et al. (1992). *Science, 255*, 419–423. Copyright 1992 AAAS.]

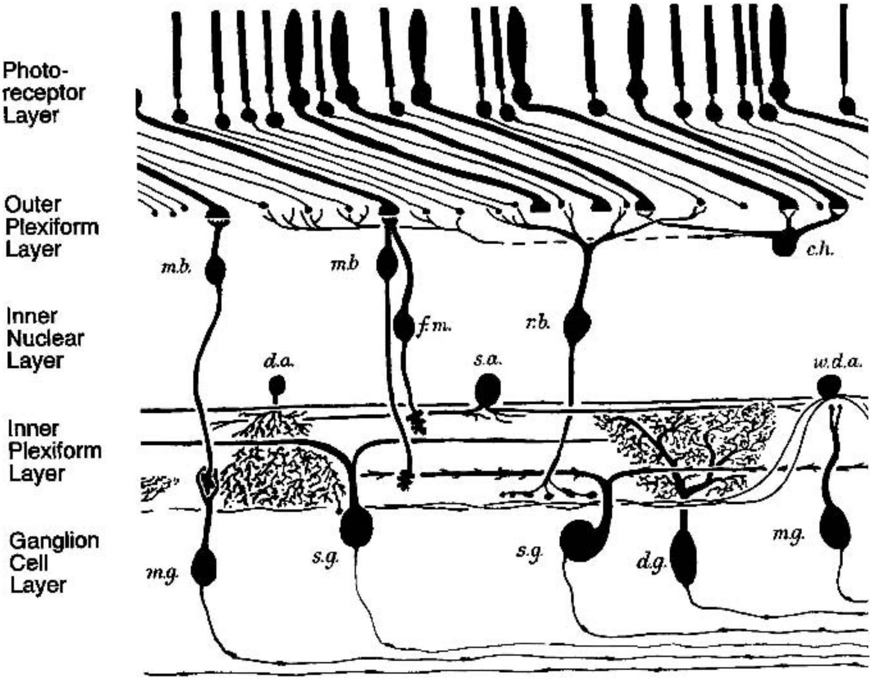

FIG. 2.5. Diagram of various cell types found in the macaque monkey and human retinas. Some ganglion cells have small dendritic arborizations (e.g., midget ganglion cells, m.g.) and others have large arborizations (e.g., stratified ganglion cells, s.g.). Abbreviations: m.b., midget bipolar cell; f.m., flat midget bipolar cell; r.b., rod bipolar cell; r.h., rod horizontal cell; d.a., diffuse amacrine cell; w.d.a., wide diffuse amacrine cell; m.g., midget ganglion cell; s.g., stratified ganglion cell; d.g., diffuse ganglion cell. [Reprinted with permission from Boycott, B.B., & Dowling, J.E. (1969). Organization of the primate retina: light microscopy. *Philosphical Transaction of the Royal Society of London. Series B. Biological sciences*, *255*, 109–184. Figure 98. (Royal Society, London)].

that needs luminance information is control of the pupil, and this is dealt with by a special class of cells that projects only to the pretectum.

The retina has five main layers (Fig. 2.5). Light is absorbed by the photoreceptors (rods and cones) that send signals to bipolar cells in the inner nuclear layer, which in turn connect to ganglion cells in the ganglion cell layer. The ganglion cells project to the lateral geniculate nucleus. Then there are two sets of cells, also with cell bodies in the inner nuclear layer, that make lateral connections. Horizontal cells make lateral connections between one photoreceptor terminal and another in the outer plexiform layer. Amacrine cells make lateral connections between one bipolar cell terminal and another in the inner plexiform layer. These lateral connections are used to compare signals from light falling on one part of the retina with signals from another part of the retina.

To understand how these comparisons are made, consider recordings from a bipolar cell, for example, the depolarizing cone bipolar cell (Fig. 2.6). The bipolar cell has a *receptive field*. The receptive field is defined as the region of visual space in which changes in luminance will affect the activity

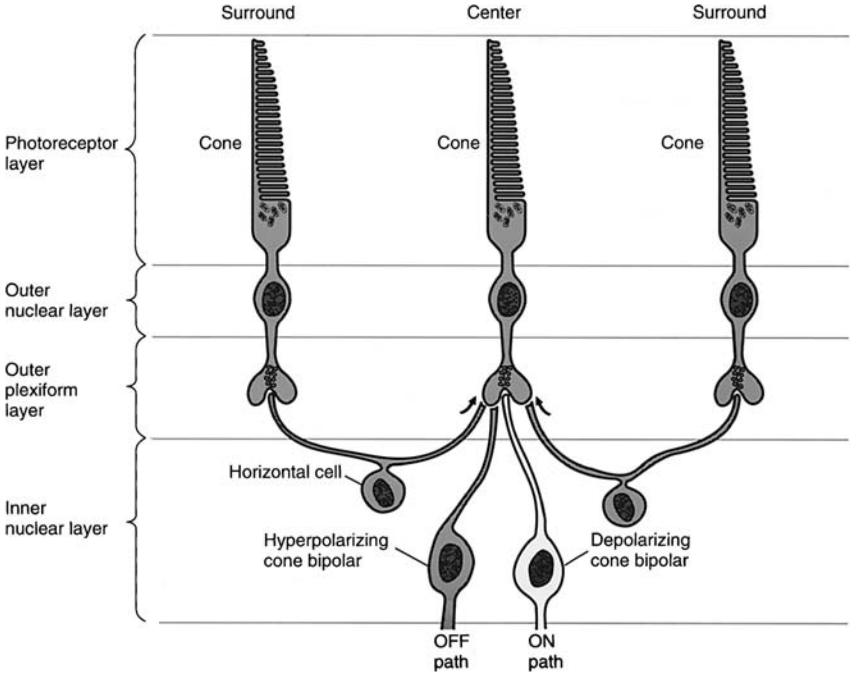

FIG. 2.6. Surround influences in the outer plexiform layer. A cone is connected to the hyperpolarizing cone bipolar cell with a sign-conserving synapse and to the depolarizing cone bipolar cell with a sign-reversing synapse (see Glossary). At the same time, cones in the surround connect to horizontal cells, which contact the cone in the center and decrease the release of transmitter from it, and consequently antagonize signals going to both types of bipolar cell. Thus, the depolarizing cone bipolar cell is depolarized by light falling on the central cone and its response is reduced when light also falls on the surround. Similarly, the hyperpolarizing cone bipolar cell is hyperpolarized by light falling on the central cone and its response is also reduced when light also falls on the surround.

of the cell. Such changes are mediated by all the parts of the retina that affect activity in the bipolar cell. Light falling on photoreceptors that are directly connected to the depolarizing cone bipolar cell will depolarize it. Light falling on photoreceptors that are connected indirectly through horizontal cells will oppose or antagonize this influence. Direct connections form the center of the receptive field, and indirect ones form the surround. Thus the bipolar cell will respond to objects falling on the center of its receptive field that are lighter than the background. In contrast, the hyperpolarizing bipolar cell responds to objects that are darker than the background through a similar process—it is hyperpolarized by light falling in the center of its receptive field and depolarized by light falling on the surround (Werblin & Dowling, 1969).

Two other properties are handled by the retina. First, a distinction is made between fine detail and movement. Second, the signals from the rods, which handle vision in dim light, and the cones, which deal with vision in bright light, are combined.

The distinction between fine detail and movement is made in the connections between bipolar cells and ganglion cells (Fig. 2.5). Some ganglion cells receive input from a limited number of bipolar cells and a limited number of photoreceptors (Polyak, 1941). They have small dendritic arborizations, small cell bodies, and give sustained responses. Thus, they have small receptive fields; that is, the area from which photoreceptors feed into them is small, and this is what gives them the ability to analyze fine detail. Examples are the midget ganglion cells in Figure 2.5. Other ganglion cells receive input from bipolar cells and photoreceptors over a wider area. They have larger dendritic arborizations, larger cell bodies, and give transient responses. Examples are the stratified ganglion cells in Figure 2.5. It is the transient nature of their response that enables them to respond to movement within their receptive field (De Monasterio & Gouras, 1975).

Bipolar cells and ganglion cells connect to each other in the inner plexiform layer with additional local and lateral connections through amacrine cells. The inner plexiform layer is divided into two sublaminae (Famiglietti & Kolb, 1976; also see Fig. 2.7). Sublamina b deals with signals for objects brighter than the background; cone bipolar cells that depolarize for such objects connect to ganglion cells that increase their firing rate when a light is turned on and are thus said to have ON responses. Sublamina a handles signals for objects that are darker than the background; cone bipolar cells that depolarize for such objects connect to ganglion cells that decrease their firing rate when a light is turned on and increase it when a light is turned off and are said to have OFF responses. Signals from the rod photoreceptors feed into this same network through rod amacrine cells, so that the ganglion cells respond in a similar fashion to both rod and cone signals.

It is the action of these bipolar and ganglion cells that is responsible for our perception of the balls in Figure 2.2. Depolarizing bipolar cells and ON center ganglion cells that receive the image of the left ball on the center of their receptive fields will fire, signaling that this ball is brighter than the background. Hyperpolarizing bipolar cells and OFF center ganglion cells that have the image of the right ball on the center of their receptive fields will fire, signaling that the right ball is darker than the background. Of course, the connections of the bipolar and ganglion cells are fairly short-range—other cells that are higher in the system, and have long-range connections, will compare the left ball with the right one, but the comparison of an object with its immediately neighboring objects is done in the retina.

The first stage of color processing also takes place within the retina. There are three types of cone photoreceptors, which absorb long-wavelength light (L), medium-wavelength light (M), and short-wavelength light (S). A class of ganglion cell called the *small bistratified ganglion cell* receives input from S cones in the ON sublamina via a blue cone bipolar cell, and input from L and M cones in the OFF sublamina via a diffuse bipolar cell. The summation of these inputs produces an ON response from blue light and an OFF response from yellow light (Dacey, 2000). The circuitry for red/green responses is not as clear, but there are ganglion cells with ON responses to red light and OFF responses to green light and vice versa (see Dacey, 2000).

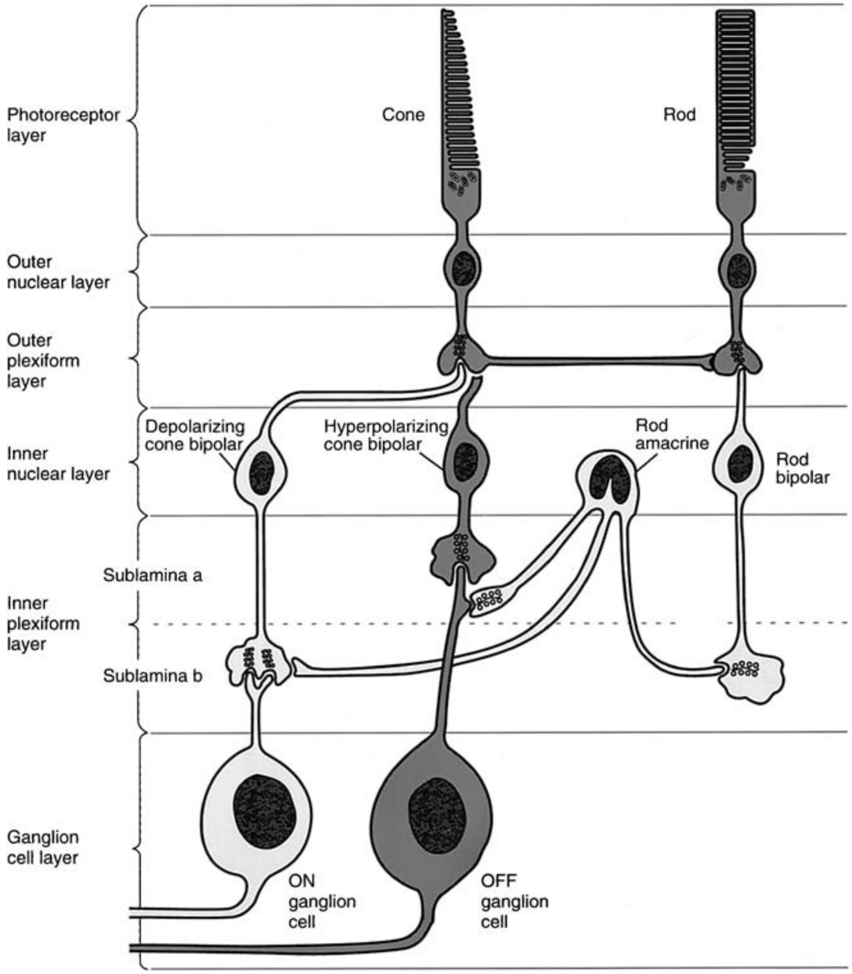

FIG. 2.7. Connections of the inner plexiform layer. Rod amacrine cells and depolarizing cone bipolar cells converge in sublamina b onto ON center ganglion cells. Hyperpolarizing bipolar cells connect to OFF center ganglion cells with a sign-conserving synapse and rod amacrine cells with a sign reversing synapse in sublamina a. Cells that depolarize in response to light are pale, and cells that hyperpolarize are shaded. Synapses between two pale cells or two shaded cells are sign conserving or excitatory; synapses between a shaded cell and a pale cell are sign reversing, or inhibitory.

The animal models that have been used to study the effects of visual deprivation are cat and monkey. This general picture is similar in the two species, except the cat has less color vision. Most of the cones in the cat are M cones; there are a few S cones but no L cones, and the percentage of color-coded cells is small. Also, the distinction between fine detail and movement is less pronounced in the cat than in the monkey. The fine detail ganglion cells are called P cells in the monkey and X cells in the cat (Enroth-Cugell & Robson, 1966), and the movement ganglion cells are called M cells in the monkey and Y cells in the cat.

Another class of ganglion cell found in the cat is called W or sluggish cells. This is a heterogeneous class of cells with a variety of different properties (Cleland & Levick, 1974; Stone & Fukuda, 1974). It includes cells that respond to brightness rather than contrast and project to the pretectum (sustained ON W cells). The main W cell projection is to the superior colliculus, the pretectum, and the suprachiasmatic nucleus. Some project to the lateral geniculate but the information from most of these cells is not sent to the primary visual cortex from there; therefore, the W cells are not part of the geniculostriate pathway. Although W cells comprise 50% of the ganglion cell population, they have small cell bodies and are not recorded very frequently in physiological experiments; therefore less is known about them. There is a class of rarely encountered cells found in the monkey that may correspond to the W cells, but their properties have not received a lot of attention (Schiller & Malpeli, 1977). Partly for this reason, and partly because most of the effects of visual deprivation are found in the geniculostriate pathway, W cells will not get much more mention in this book.

3. Function in the Lateral Geniculate Nucleus

The lateral geniculate nucleus (LGN) receives signals from the retina and transmits them on to the cortex without much processing. Signals from the left and right eyes remain segregated in different layers in the lateral geniculate (Fig. 2.8). In the macaque there are six layers: four dorsal with small cells, called the parvocellular layers (P), and two ventral with large cells called magnocellular (M). The fine detail cells project from the retina to the P layers, and the movement cells to the M layers, as reflected in the terminology for these two groups of cells (see Fig. 2.8). Counting from the bottom, layers 1, 4, and 6 receive input from the contralateral eye, and layers 2, 3, and 5 from the ipsilateral eye.

The properties of cells in the lateral geniculate are very like those of the cells in the retina that project to them (Wiesel & Hubel, 1966). There are cells that are excited by light in the center of their receptive field and inhibited by light in the surrounding area; these are ON center cells, just as in the retina. There are cells whose activity is reduced by light in the center and increased by light in the surround; these are OFF center cells. There are red/green and yellow/blue color-coded cells. There does not seem to be much convergence from different cell types in the retina onto single cells in the lateral geniculate. The main difference between the LGN and retinal cells that has been noted is that LGN cells give less response to white light illuminating the whole receptive field uniformly. This occurs because there are additional inhibitory interneurons in the lateral geniculate, so that antagonism from the surround of the receptive field of a cell more closely balances the center.

The lateral geniculate receives input from the various modulatory pathways located in the brainstem: noradrenaline input from the locus coeruleus, serotonin input from the raphe nuclei, and acetylcholine input from the parabrachial region (Sherman & Koch, 1986). It also receives some input from the eye movement system. These inputs modulate signals reaching the cortex

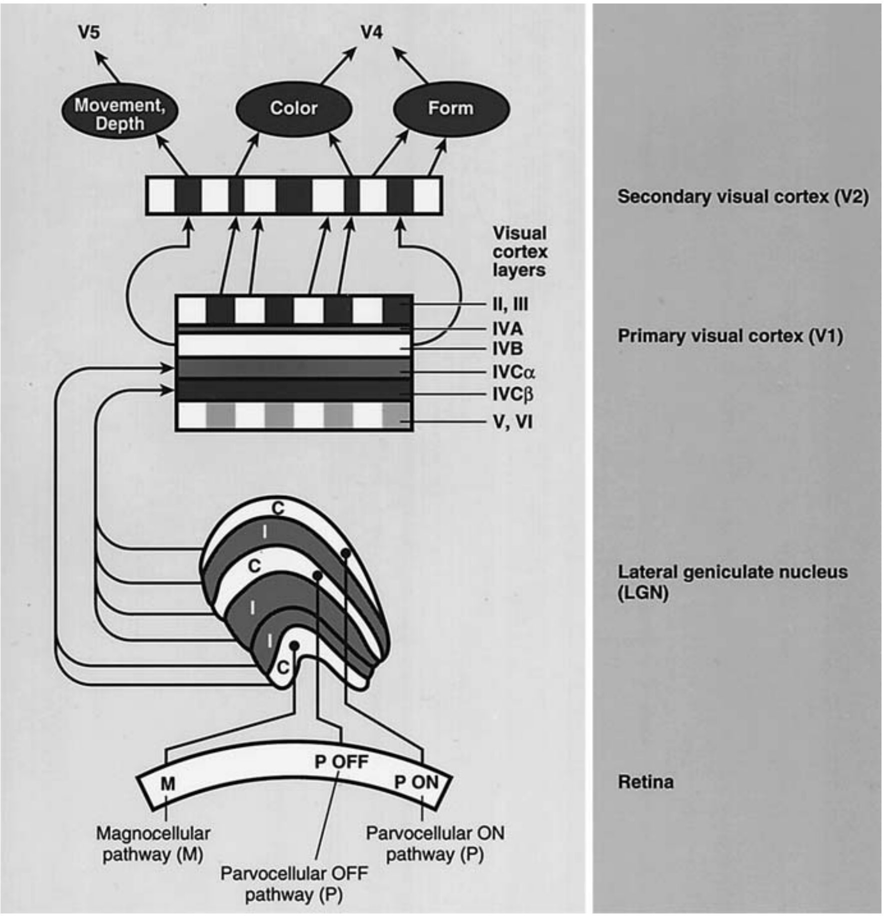

FIG. 2.8. Streams of processing for color, form, disparity, and movement between the retina and the visual cortex. The M pathway projects to the two lower layers of the lateral geniculate nucleus, next to layer IVC and then to layer IVB in the primary visual cortex. The signal is then passed to area V5 and the thick stripes in the secondary visual cortex. The P pathway projects to the upper four layers of the lateral geniculate nucleus with a preponderance of ON center cells in the upper two layers and OFF center cells in the middle two layers, and then to layer IVCß. The pathway splits into two streams; one deals with color, projecting from the blobs in layers II and III of the primary visual cortex to the thin stripes in the secondary visual cortex, and then to V4. The other deals with form, projecting from the interblob areas to the pale stripes in V2 and an area near V4. Input from the contralateral (C) retina is shown. Input from the ipsilateral (I) retina projects to the neighboring layers in the LGN.

by affecting attention and by directly inhibiting signals while saccadic eye movements are being made. The modulatory signals, and interactions between the visual cortex and lateral geniculate, are also responsible for the depolarization of lateral geniculate neurons that characterizes the transition from a state of sleep to a state of arousal (McCormick & Bal, 1997). Essentially, the function of the lateral geniculate nucleus is to gate signals going from the retina to the cortex, rather than to process them.

4. Function in the Visual Cortex

The visual cortex is the place where objects in and out of their visual context are analyzed in detail. For the analysis of form, there are cells that respond to the edges, curvature, and corners of objects. For the analysis of movement, there are cells that respond to the direction of movement, and to the direction of movement in relation to the background. For the analysis of color, there are cells that respond to wavelengths coming from an object in relation to wavelengths coming from objects nearby and to an average of the wavelengths from objects in other parts of the field of view.

The visual cortex is the first location in which signals from the two eyes converge onto a single cell. Signals from each eye in layer IV are kept largely separate in the adult, but the monocular cells in layer IV converge onto binocular cells in layers II, III, V, and VI. This is a statistical matter rather than an absolute matter—there are some binocular cells in layer IV and some monocular cells in layers II, III, V, and VI—but the tendency is clear. Consequently, visual cortex is the first location where one finds cells sensitive to disparity, that is, cells responding to objects nearer than the point of fixation and cells responding to objects further than the point of fixation (Poggio, Gonzalez, & Krause, 1988).

To a certain extent, form, color, movement, and disparity are dealt with by separate groups of cells. Because of this, layer IV, which is the input layer for the cortex, is more complicated in visual cortex than in any other area of cortex (Fig. 2.8). It is divided into sublayers IVA, IVB, IVCα, and IVCß. Projections from the movement cells in the magnocellular layers of the lateral geniculate come into layer IVCα, which projects to layer IVB. Layer IVB projects to secondary visual cortex (V2 and V5), and is therefore an output layer rather than an input layer. Cells in V2 that handle disparity also project on to V5, alias MT, which consequently deals with movement, disparity, and movement in depth (Zeki, 1978; Britten, 2004).

The cells in the parvocellular layers of the lateral geniculate, dealing with color and fine detail, project to layers IVCß and IVA (Fig. 2.8). These signals are analyzed further in other layers of the primary visual cortex. If one makes a horizontal section through primary visual cortex in layers III and II, and stains it for cytochrome oxidase, a mitochondrial enzyme that is found in areas of high metabolic activity, one finds patches of stain known as blobs. Color-coded cells without orientation selectivity are concentrated in the blobs, while the cells in the areas between the blobs respond to the orientation of an edge, and have less color selectivity (Livingstone & Hubel, 1984).

In the secondary visual cortex (V2), cells dealing with color, form, and disparity are also kept somewhat separate. If one stains V2 with cytochrome oxidase and cuts a horizontal section, one finds three sets of stripes: thick, thin, and pale stripes. The thin stripes process surface properties such as color and brightness, cells specific for disparity are concentrated in the thick stripes, and cells specific for orientation are concentrated in the pale stripes (Hubel & Livingstone, 1987; Roe, 2003). The thin stripes project to an area called V4, which deals particularly with color and form, and the thick stripes project to V5 and MST (DeYoe & van Essen, 1985). However, it should be emphasized that these concentrations of cells that process similar information and the projections described here are the predominant ones; there are also interconnections between the pathways for color, form, disparity, and movement (see Sincich & Horton, 2002; Ts'o, Roe, & Gilbert, 2001; Xiao & Felleman, 2004). This is to be expected because one can see, for example, depth, form, and movement in equiluminant color boundaries, although less easily than in luminance boundaries.

4.1. Columnar Organization of Cortex

The cerebral cortex is a two-dimensional sheet, 2 mm thick and with enough area to cover a large room. Within the 2-mm thickness, cells located above and below each other in the cortex tend to have similar properties. This is true in all parts of cortex, and was noticed first in the somatosensory cortex (Mountcastle, 1957), and later in the visual cortex of the cat (Hubel & Wiesel, 1962). Consequently the cortex is said to be organized into columns. The similar properties of the cells within a cortical column are most likely due to the arrangement of anatomical connections, which run primarily in a vertical direction.

In the monkey, there are columns for ocular dominance, color, and the orientation of edges (Livingstone & Hubel, 1984). While the cells in layers II, III, V, and VI tend to be binocular, they also tend to be dominated by one eye. A cell dominated by the left eye in layer II will tend to lie above axon terminals from the left eye in layer IV, and a cell dominated by the right eye in layer VI will tend to be below axon terminals from the right eye in layer IV, and so on. Color-coded cells in layer V or VI tend to lie under the blobs, which are located in layers III and II. When it comes to orientation, there are cells specific for vertical edges, for horizontal edges, and for a variety of orientations in between. Again, cells that lie in layers V and VI and are specific for vertical edges tend to be positioned below cells in layers II and III that are also specific for vertical edges. These cells are organized into *orientation columns.*

Every point in the field of view of each eye has to be analyzed for color and orientation, so the sets of columns overlap. The cytochrome oxidase blobs are lined up in the centers of the ocular dominance columns (Horton & Hubel, 1981; Fig. 2.9). The orientation columns are arranged around features, called pinwheels, which also tend to lie in the center of ocular dominance columns in both cat and monkey (Fig. 2.10). However, the centers of the pinwheels do not necessarily line up with the cytochrome oxidase blobs seen in the macaque (Bartfeld & Grinvald, 1992). The organization in the cat primary visual cortex is very like that of the macaque, except that color cells are absent (color-coded cells are mostly in the W cell projection, in the extrastriate pathway), so there are just two sets of overlapping columns for orientation and ocular dominance. The movement system, in area 17 of the primate, is an exception to the general rule of columnar processing; signals come in to layer IVCα, project to layer IVB, and then out of the primary visual cortex. However, this is the only known exception; in all other parts of cortex, processing is

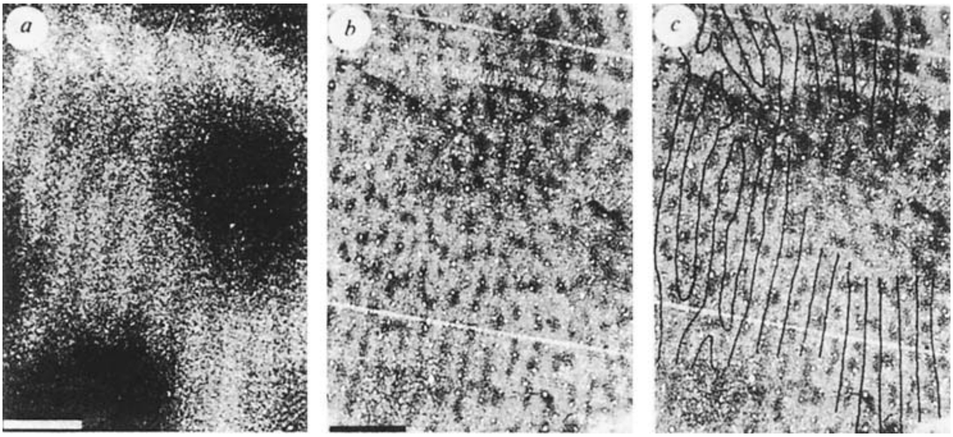

FIG. 2.9. (A) Dark-field autoradiograph of the striate cortex in a normal macaque showing ocular dominance columns. Section is tangential, grazing layer V (*dark ovals*) but passing mainly through layer IVC. (B) More superficial section from the same tissue block showing cytochrome oxidase patches. (C) Borders of the columns from (A) superimposed on (B). [Reprinted with permission from Horton, J. C., & Hubel, D. H. (1981). *Nature, 292*, 762.]

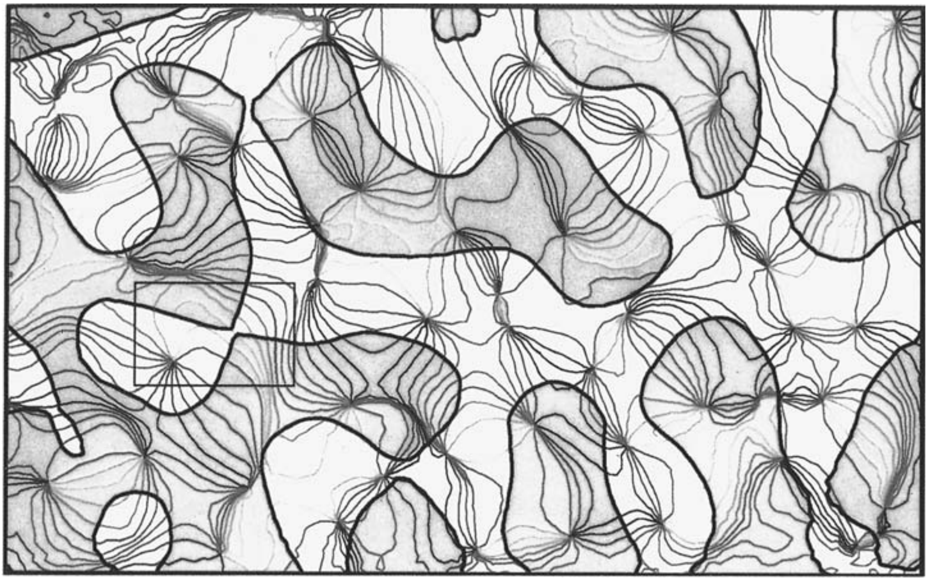

FIG. 2.10. Relationship between ocular dominance and orientation maps in the cat. Thick lines show the outlines of the ocular dominance columns. Thin lines join cells with the same orientation specificity. The pinwheels formed by these lines coming together tend to be centered on the ocular dominance columns. [Reprinted with permission from Hubener, M., et al. (1997). *Journal of Neuroscience*, *17*, 9270–9284. Copyright 1997 Society for Neuroscience.]

columnar. A patch of cortex that contains the machinery to represent a single location in space (i.e., that analyzes signals in terms of ocular dominance, all colors, and all orientations) is known as a *hypercolumn*.

The visual properties dealt with in columns in V2 are not too different from the columnar properties of V1. As mentioned above, the thin stripes of cytochrome oxidase staining handle the surface properties of color and brightness, the pale stripes deal with orientation and form, and the thick stripes deal with disparity and movement. Most cells are driven binocularly—indeed a number can only be driven binocularly—so that in V2 ocular dominance is no longer a factor (Hubel & Livingstone, 1987). The thin stripes contain patches within which all colors are represented, arranged as they are in the spectrum (Xiao, Wang, & Felleman, 2003). The thick stripes contain columns for disparity, and both thick and pale stripes contain columns for orientation (Ts'o et al., 2001). Further details will undoubtedly emerge as more experiments are done.

Beyond V2, the parameters of the stimulus handled within columns is less clear. Obviously the parameters will change with the visual area because different visual areas deal with different properties of the stimulus. In V4, there may be separate columns for red, green, and blue (Zeki, 1977) although this is no longer certain. In V5, there are columns for direction of movement (Albright, Desimone, & Gross, 1984), for movement of objects in relation to the background as opposed to movement of the whole field of view (Born & Tootell, 1992), and for disparity (DeAngelis & Newsome, 1999). Further physiological details remain to be worked out in areas V4 and V5 and are completely unknown for the other 30 areas of the visual cortex, but every anatomical experiment that has been done shows punctate projections from one area to another, strongly suggesting the existence of columns everywhere.

5. Parallel Processing within the Visual System

It should be clear by now that different features of the visual stimulus are dealt with in parallel in the visual system. Signals for objects brighter than the background and signals for objects darker than the background are kept separate through four levels of processing—the bipolar cell, ganglion cell, lateral geniculate cell, and the first stage within V1—before being combined to analyze the orientation and direction of movement, independent of contrast (Fig. 2.8). Signals for color and for movement are partially separate through at least five levels of processing: the ganglion cell, lateral geniculate, V1, V2, and V4/V5. Signals for color and for form are partially separate through at least three levels of processing: V1, V2, and V4 (the area for processing form in the macaque at the level of V4 is still being identified, but it seems likely from deficits found in humans that there are separate areas for color and form at this level).

Very likely, parallel processing will continue to be found as higher levels of the cortex are analyzed. Depth perception remains to be worked out. Helmholtz listed a number of cues to depth perception, including disparity, convergence, accommodation, size, haze, interposition, and motion parallax. How the various cues to depth perception are analyzed and brought together is largely unknown. Cells sensitive for disparity are found in V1, in the thick stripes of V2, and in V3, V4, and V5. There are separate columns for near and far cells in V2, but how these are brought together with the other cues is largely unknown. Whatever the final details, it seems extremely likely that depth perception will be analyzed by columns in a parallel fashion because of the variety of cues that have to be evaluated and then combined.

6. Hierarchical Processing within the Visual System

What happens to the signals as they get transmitted within these parallel pathways and are processed along the way? The first experiments were done by Hubel and Wiesel (1962) and concerned the analysis of form in the cat. They recorded single cells in the visual cortex with a microelectrode in anesthetized paralyzed animals. Interestingly, the cells responded much more vigorously to bars and edges, particularly moving ones, than to lights turned on and off. There were cells that responded to orientation, with separate cells responding to lines brighter than the background and lines darker than the background. They called these *simple cells*, because their properties could be explained simply by input from a series of lateral geniculate cells lined up along the axis of the orientation (Fig. 2.11). They also found cells that responded to orientation independent of contrast, which they called *complex cells*, and proposed that they receive input from simple cells. The simple and complex cells responded to long bars, but other cells responded to short ones due to the influence of inhibitory signals, and these were called *hypercomplex*. Subsequently, investigators have found that the complex cells actually receive direct input from the lateral geniculate (see Stone, 1983), but the basic idea of a hierarchical organization in these cell types is nonetheless probably true.

Clearer evidence for a hierarchy of cell types comes from the color system (Daw, 1984). Photoreceptors converge onto the opponent color cells which

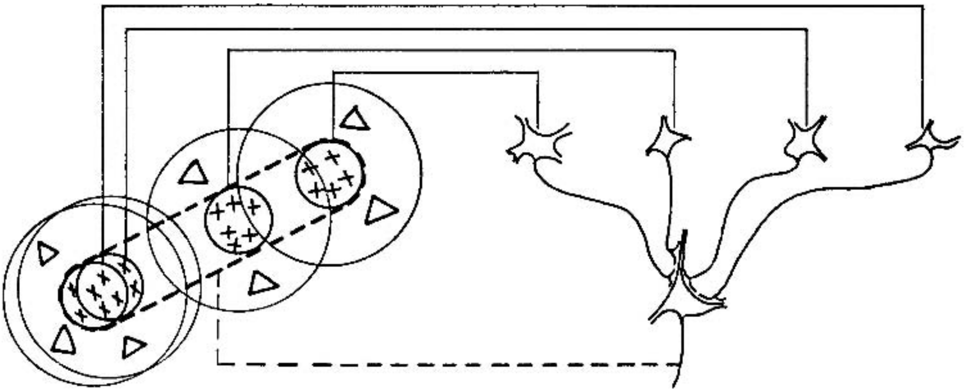

FIG. 2.11. Scheme for producing simple cells from the lateral geniculate input to the cortex. Four lateral geniculate cells with ON centers, positioned along a line, make excitatory connections with a cell in the cortex. The cortical cell will then respond to a line oriented along the 2 o'clock/8 o'clock axis. [Reprinted with permission from Hubel, D. H., & Wiesel, T. N. (1962). *Journal of Physiology*, *160*, 106–154. Blackwell Publishing.]

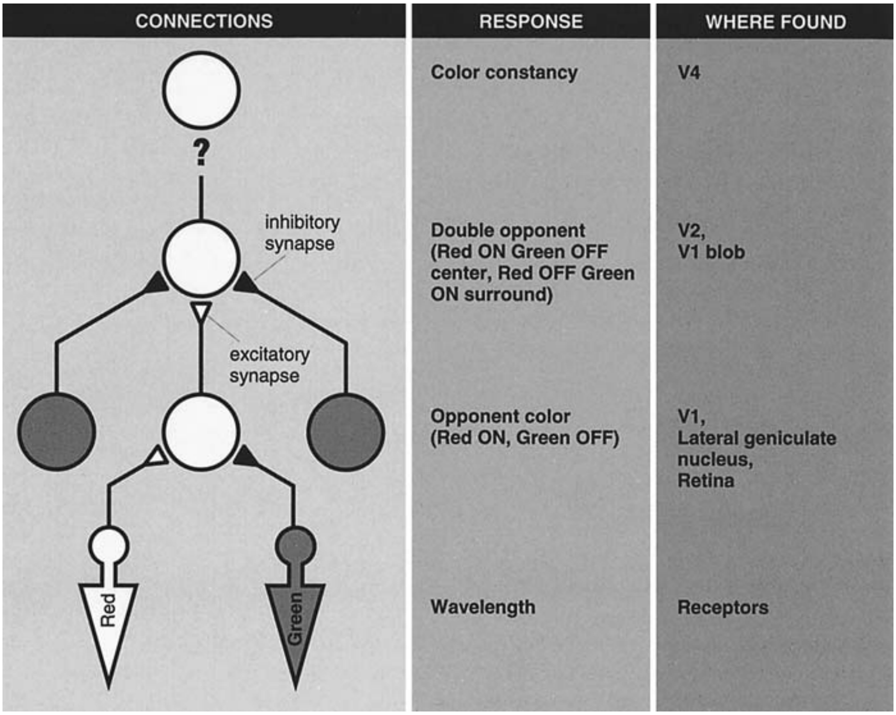

FIG. 2.12. The first three stages in the processing of color vision. Red-absorbing cones excite bipolar cells and green cones inhibit them, to produce bipolar cells, ganglion cells, lateral geniculate cells, and cells in layer IVCß that give an ON response to red and an OFF response to green. Red ON, green OFF cells in the center of the receptive field excite the double opponent cell and red ON/green OFF cells in the surround inhibit it. This produces a cell that has an ON response to red and OFF response to green in the center, with an OFF response to red and ON response to green in the surround, because the sign of the response is reversed in the surround by the inhibitory synapse. Double opponent cells do not respond to uniform illumination (in the example illustrated, excitation from red in the center will be cancelled by inhibition from red in the periphery, and excitation from green in the periphery will be cancelled by inhibition from green in the center). Double opponent cells also do not respond to white light, because the input from the red receptors will be cancelled by the input from the green receptors. The synaptic organization between V1, V2, and V4 is not known, but the cells in V4 give a response that corresponds to object color constancy. *Open triangles* represent excitatory synapses, *solid triangles* inhibitory synapses.

respond positively to some wavelengths and negatively to others (see Fig. 2.12). Within the color system, bipolar cells, ganglion cells, lateral geniculate cells, and cells within layer IVCß of the cortex all include opponent color cells. At the next stage, in the blobs in V1, opponent color cells converge to form double opponent cells. These are cells that are opponent for color and also for space so that they respond to color contrasts and some spatial contrasts, but not to uniform illumination (see caption to Fig. 2.12). The response of a red/green double opponent cell to a grey spot in a green surround is the same as its response to a red spot in a grey surround; grey will activate both red and green receptors, with responses that will cancel each other, while red in the center and green in the surround will both excite the cell. Because a grey spot in a green surround appears reddish (this is called

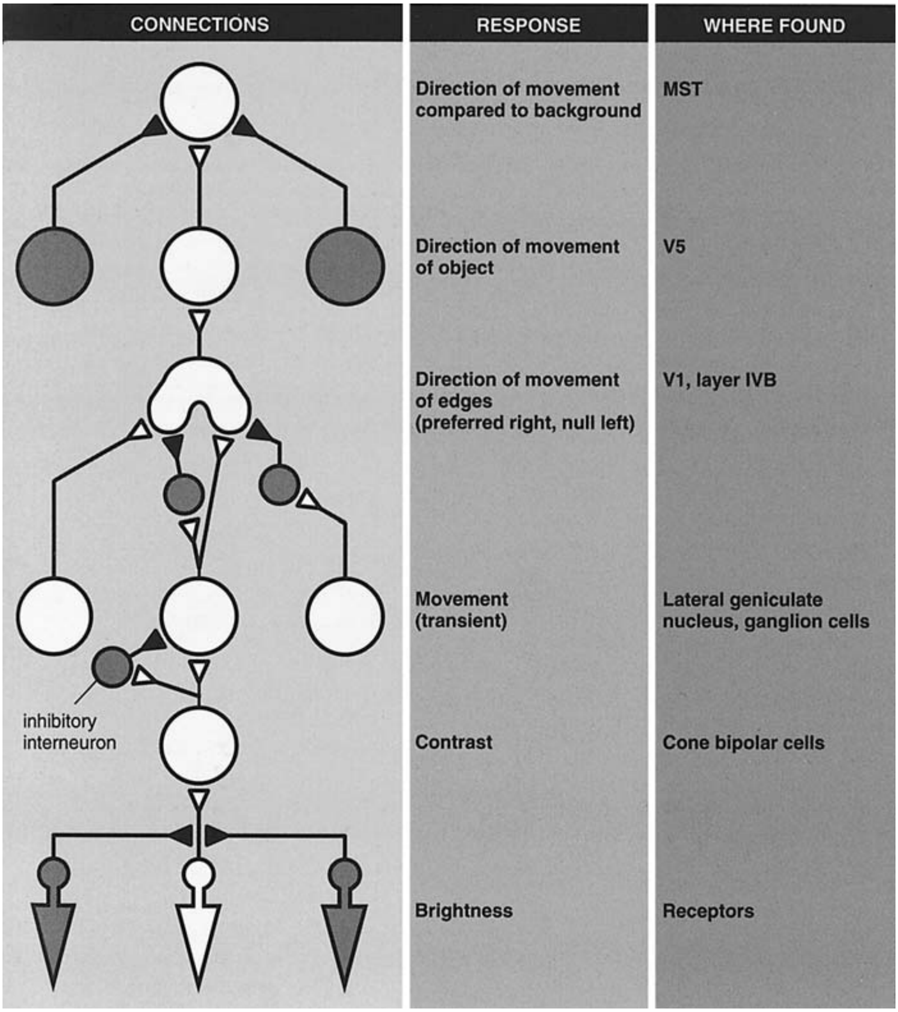

FIG. 2.13. First five stages in the processing of movement information. Receptors respond to brightness and bipolar cells to contrast. Some circuit, perhaps a local inhibitory circuit, makes the response of the movement ganglion cells transient, and consequently the response of the movement lateral geniculate cells that follow them is also transient. Lateral inhibitory connections within the visual cortex reduce the response in one direction to produce direction-selective cells. The synaptic circuitry that produces a cell specific for the movement of the object, as opposed to the movement of the contours within the object, is not known, and is therefore left out. Presumably the direction of movement of the object in relation to its background is produced by excitatory connections from the direction-selective cells that process the object, and inhibitory connections from the direction-selective cells that process the background. *Open triangles* represent excitatory synapses, *solid triangles* inhibitory synapses.

simultaneous color contrast) double opponent cells explain the phenomenon of simultaneous color contrast (Daw, 1967).

Simultaneous color contrast is a local phenomenon, whereas object color constancy involves comparisons over a large part of the field of view. Cells in V1 have small receptive fields, whereas cells in V4 have large ones. Cells in V4 are affected by an average of the wavelengths coming from objects in a wide area of the field of view. Thus it seems likely that the double opponent cells in V1 converge onto cells in V2, and these converge again onto cells in V4 to give object color constancy (Zeki, 1983).

Evidence for a hierarchy of cell types is also clear in the movement system (Fig. 2.13). Cells in the magnocellular pathway in the retina and lateral geniculate respond to movement. In the primary visual cortex, one finds cells that respond to *direction* of movement; this response is generated because of lateral inhibitory connections that prevent the cell from responding to inappropriate directional movement. In V5, there are cells that respond to movement of the complete object, as opposed to movement of the individual contours of the object (Movshon, Adelson, Gizzi, & Newsome, 1985). There are also cells that respond to movement of an object in relation to the background, rather than movement of the object itself (Tanaka, Hikosaka, Saito, Yukie, Fukada, & Iwai, 1986; see Fig. 2.14). One can also distinguish first-order movement, defined by luminance, from second-order movement, defined by contrast. Functional magnetic resonance imaging (fMRI) studies in humans and data from brain lesions have demonstrated that first-order movement is computed in V1, whereas second-order movement is computed in higher visual areas (see Dumoulin, Baker, Hess, & Evans, 2003).

Stereoscopic depth perception is also arranged in a hierarchical fashion. The cells in V1 that are sensitive to disparity respond to absolute disparity. Cells in V2 and V5, on the other hand, respond to relative disparity (see Parker, 2004). Various behavioral and stimulation experiments show that V5 is involved in depth perception and in movement in depth. It seems likely, therefore, that V5 is the area where disparity cues and movement cues are brought together to produce a perception of the trajectory in space. However, the differences in receptive field properties between V2 and V5/MT and also between V5/MT and the areas that it projects to (MST and FST) remain to be detailed.

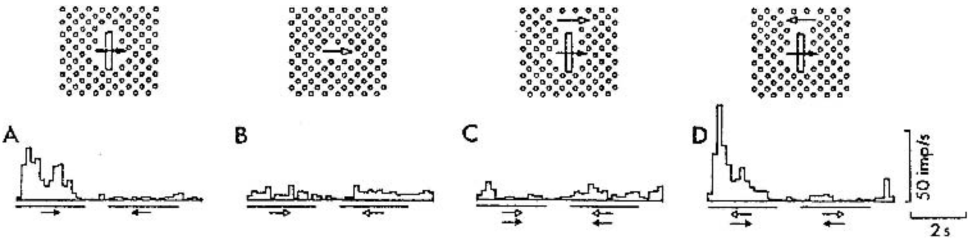

FIG. 2.14. Cell that responds to the movement of an object against the background. (A) Response to movement of bar. (B) Response to movement of background. (C) Response to movement of bar and background together in the same direction. (D) Response to movement of bar and background in opposite directions. Notice that movement of the bar against the background gives the largest response, and movement of the bar with the background gives little response. [Reprinted with permission from Tanaka, K., et al. (1986). *Journal of Neuroscience*, *6*, 134–144. Copyright 1986, Society for Neuroscience.]

7. Summary

It is hoped that this brief summary will give an idea of how the visual system is organized. There are signal streams processed by cells that handle broad aspects of the visual input, with the details analyzed in parallel within the streams.

In the color stream, red/green, yellow/blue, and black/white aspects are processed in parallel. As one goes up the system, a comparison is first made between the long, medium, and short wavelength bands coming from a small area in the field of view. This is then compared with the wavelengths from the area in the immediate surround, and then with those from a large part of the field of view to create the perception of object color constancy.

In the form stream, objects lighter than the background and darker than the background are distinguished first. The orientation of edges and lines is analyzed, then the length of segments of the edges and lines. Finally, this analysis of an object's components has to be integrated into the perception of the object's form and shape.

In the movement stream, the response within the retina is transient, enabling movement to be detected. Lateral inhibitory connections operate on signals from the brighter-than-background pathway and from the darker-than-background pathway to give the direction of movement; these signals are then brought together to create the perception of direction of movement independent of contrast. Next, signals for the direction of movement of contours are combined to give the direction of movement of the whole object. Then the direction of movement of the object in relation to the background is distinguished from direction of movement of the object by itself.

In the depth system, disparity is detected immediately after signals from the two eyes come together in the cortex. There are cells specific for objects nearer than the fixation point and for objects further away than the fixation point. Disparity is actually a relative phenomenon, like brightness and color, and cells specific for relative disparity have been described in V2. However, how disparity is related to other cues about depth perception is unknown.

The concentration on streams of processing in this description is an oversimplification. For example, edges can be detected between two colored objects of equal luminance, showing that color signals enter the form pathway. Although some displays of stereopsis fail when one object is seen in relation to another of equal luminance, other displays succeed. Consequently, perception experiments suggest that there must be connections between the various streams and the anatomy proves that there are. However, the division of the visual system into streams of signal processing is a useful concept for understanding the overall organization.

References

Albright, T. D., Desimone, R., & Gross, C. G. (1984). Columnar organization of directionally selective cells in visual area MT of the macaque. *Journal of Neurophysiology, 51*, 16–31.

Bartfeld, E., & Grinvald, A. (1992). Relationships between orientation-preference pinwheels, cytochrome oxidase blobs, and ocular dominance columns in primate striate cortex. *Proceedings of the National Academy of Sciences of the United States of America, 89*, 11905–11909.

Born, R. T., & Tootell, R. H. (1992). Segregation of global and local motion processing in primate middle temporal visual area. *Nature, 357*, 497–499.

Boycott, B. B., & Dowling, J. E. (1969). Organization of the primate retina: light microscopy. *Philosophical Transaction of the Royal Society of London. Series B. Biological sciences, 255*, 109–184.

Britten, K. H. (2004). The middle temporal area: motion processing and the link to perception. In L. M. Chalupa & J. S. Werner (Eds.), *The Visual Neurosciences* (pp. 1203–1216). Cambridge, MA: MIT Press.

Cleland, B. G., & Levick, W. R. (1974). Properties of rarely encountered types of ganglion cells in the cat's retina and an overall classification. *Journal of Physiology, 240*, 457–492.

Dacey, D. M. (2000). Parallel pathways for spectral coding in primate retina. *Annual Review of Neuroscience, 23*, 743–775.

Daw, N. W. (1967). Goldfish retina: organization for simultaneous color contrast. *Science, 158*, 942–944.

Daw, N. W. (1984). The psychology and physiology of colour vision. *Trends in Neurosciences, 7*, 330–336.

DeAngelis, G. C., & Newsome, W. T. (1999). Organization of disparity-selective neurons in macaque area MT. *Journal of Neuroscience, 19*, 1398–1415.

De Monasterio, F. M., & Gouras, P. (1975). Functional properties of ganglion cells of the rhesus monkey retina. *Journal of Physiology, 251*, 167–195.

DeYoe, E. A., & Van Essen, D. C. (1985). Segregation of efferent connections and receptive field properties in visual area V2 of the macaque. *Nature, 317*, 58–61.

Dumoulin, S. O., Baker, C. L., Hess, R. F., & Evans, A. C. (2003). Cortical specialization for processing first- and second-order motion. *Cerebral Cortex, 13*, 1375–1385.

Enroth-Cugell, C., & Robson, J. G. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *Journal of Physiology, 187*, 517–552.

Famiglietti, E. V., & Kolb, H. (1976). Structural basis for ON- and OFF-center responses in retinal ganglion cells. *Science, 194*, 193–195.

Horton, J. C., & Hubel, D. H. (1981). Regular patchy distribution of cytochrome oxidase staining in primary visual cortex of macaque monkey. *Nature, 292*, 762–764.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology, 160*, 106–154.

Hubel, D. H., & Livingstone, M. S. (1987). Segregation of form, color, and stereopsis in primate area 18. *Journal of Neuroscience, 7*, 3378–3415.

Hubener, M., Shoham, D., Grinvald, A., & Bonhoeffer, T. (1997). Spatial relationships among three columnar systems in cat area 17. *Journal of Neuroscience, 17*, 9270–9284.

Kaufman, L. (1974). *Sight and mind.* New York: Oxford University Press.

Kuffler, S. W. (1953). Discharge patterns and functional organization of mammalian retina. *Journal of Neurophysiology, 16*, 37–68.

Livingstone, M. S., & Hubel, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience, 4*, 309–356.

McCormick, D. A., & Bal, T. (1997). Sleep and arousal: thalamocortical mechanisms. *Annual Review of Neuroscience, 20*, 185–215.

Mountcastle, V. B. (1957). Modality and topographic properties of single neurons of cat's somatic sensory cortex. *Journal of Neurophysiology, 20*, 408–434.

Movshon, J. A., Adelson, E. H., Gizzi, M. S., & Newsome, W. T. (1985). The analysis of moving visual patterns. In C. Chaga, R. Gattass, & C. Gross (Eds.), *Pattern recognition mechanisms* (pp. 117–151). Vatican City: Pontifical Academy of Sciences.

Parker, A. J. (2004). From binocular disparity to the perception of stereoscopic depth. In L. M. Chalupa, & J. S. Werner (Eds.), *The visual neurosciences* (pp. 779–792). Cambridge, MA: MIT Press.

Pasupathy, A., & Connor, C. E. (2002). Population coding of shape in area V4. *Nature Neuroscience, 5*, 1332–1338.

Poggio, G. F., Gonzalez, F., & Krause, F. (1988). Stereoscopic mechanisms in monkey visual cortex: binocular correlation and disparity selectivity. *Journal of Neuroscience, 8*, 4531–4550.

Polyak, S. L. (1941). *The retina.* Chicago: University of Chicago Press.

Roe, A. W. (2003). Modular complexity of area V2 in the macaque monkey. In C. Collins, & J. H. Kaas (Eds.), *The primate visual system* (pp. 109–138). New York: CRC Press.

Rosenquist, A. C. (1985). Connections of visual cortical areas in the cat. In A. Peters, & E. G. Jones (eds.), *Cerebral cortex* (pp. 81–117). New York: Plenum.

Schiller, P. H., & Malpeli, J. G. (1977). Properties and tectal projections of monkey ganglion cells. *Journal of Neurophysiology, 40*, 428–445.

Sherman, S. M., & Koch, C. (1986). The control of retinogeniculate transmission in the mammalian lateral geniculate nucleus. *Experimental Brain Research, 63*, 1–20.

Sincich, L. C., & Horton, J. C. (2002). Divided by cytochrome oxidase: a map of the projections from V1 to V2 in macaques. *Science, 295*, 1734–1737.

Stone, J. (1983). *Parallel processing in the visual system.* New York: Plenum Press.

Stone, J., & Fukuda, Y. (1974). Properties of cat retinal ganglion cells: a comparison of W-cells with X- and Y-cells. *Journal of Neurophysiology, 37*, 722–748.

Tanaka, K., Hikosaka, K., Saito, H. E., Yukie, M., Fukada, Y., & Iwai, E. (1986). Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *Journal of Neuroscience, 6*, 134–144.

Ts'o, D. Y., Roe, A. W., & Gilbert, C. D. (2001). A hierarchy of the functional organization for color, form and disparity in primate visual area V2. *Vision Research, 41*, 1333–1349.

Ungerleider, L. G., & Pasternak, T. (2004). Ventral and dorsal cortical processing streams. In L. M. Chalupa, & J. S. Werner (Eds.), *The visual neurosciences* (pp. 541–562). Cambridge, MA: MIT Press.

Van Essen, D. C., Anderson, C. H., & Felleman, D. J. (1992). Information processing in the primate visual system: an integrated systems perspective. *Science, 255*, 419–423.

Werblin, F. S., & Dowling, J. E. (1969). Organization of the retina of the mudpuppy, *Necturus maculosus.* II. Intracellular recording. *Journal of Neurophysiology, 32*, 339–355.

Wiesel, T. N., & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *Journal of Neurophysiology, 29*, 1115–1156.

Xiao, Y. P., Wang, Y., & Felleman, D. J. (2003). A spatially organized representation of colour in macaque cortical area V2. *Nature, 421*, 535–539.

Xiao, Y. P., & Felleman, D. J. (2004). Projections from primary visual cortex to cytochrome oxidase thin stripes and interstripes of macaque visual area 2. *Proceedings of the National Academy of Sciences of the United States of America, 101*, 7147–7151.

Zeki, S. M. (1977). Colour coding in the superior temporal sulcus of the rhesus monkey visual cortex. *Proceedings of the Royal Society of London. Series B. Biological sciences, 197*, 195–223.

Zeki, S. M. (1978). Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *Journal of Physiology, 277*, 273–290.

Zeki, S. M. (1983). Colour coding in the cerebral cortex: the reaction of cells in monkey visual cortex to wavelengths and colours. *Neuroscience, 9*, 741–765.