Inaugural Article: Parallel information processing channels created in retina

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Parallel information processing channels created in the retina

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Contributed by Peter H. Schiller, August 13, 2010 (sent for review July 10, 2010)

In the retina, several parallel channels originate that extract different attributes from the visual scene. This review describes how these channels arise and what their functions are. Following the introduction four sections deal with these channels. The first discusses the "ON" and "OFF" channels that have arisen for the purpose of rapidly processing images in the visual scene that become visible by virtue of either light increment or light decrement; the ON channel processes images that become visible by virtue of light increment and the OFF channel processes images that become visible by virtue of light decrement. The second section examines the midget and parasol channels. The midget channel processes fine detail, wavelength information, and stereoscopic depth cues; the parasol channel plays a central role in processing motion and flicker as well as motion parallax cues for depth perception. Both these channels have ON and OFF subdivisions. The third section describes the accessory optic system that receives input from the retinal ganglion cells of Dogiel; these cells play a central role, in concert with the vestibular system, in stabilizing images on the retina to prevent the blurring of images that would otherwise occur when an organism is in motion. The last section provides a brief overview of several additional channels that originate in the retina.

midget channels | ON/OFF channels | parasol channels

In the past 120 years, great strides have been made in uncovering how the brain processes visual information. Several of the discoveries were quite surprising and unexpected. It was found that, in the retina, the photoreceptors faced away from the incoming light and were closest to the pigment epithelium. All the other cell types in the retina were positioned between the photoreceptors and the vitreous humor. This meant that, except for the central foveal region, the retina is arranged: an excitatory center area and an antagonistic center-surround organization form a basic ground plan for the visual systems of all vertebrates.

ON and OFF Channels

Origins of the ON and OFF Channels in the Retina. In the 1960s, it became possible to place finely drawn micropipettes inside the various cell types of the retina (10, 11). Such intracellular recordings provided accurate measurements of the graded potentials produced by the neurons and made possible their subsequent anatomical identification by minute dye injections. Studies using these procedures, beginning with the pioneering work in John Dowling’s laboratory, revealed that the basic organization of the retina in vertebrate species is quite similar (12–16). The photoreceptors in all cases hyperpolarize to light and use the neurotransmitter glutamate, which acts differently on the two major classes of bipolar cells: OFF bipolars, which have sign-conserving ionotropic receptors (iGluRs), and ON bipolars, which have sign-inverting metabotropic receptors (mGluRs). Thus, the OFF cells polarize in the same manner as do the photoreceptors whereas the ON bipolars polarize in the direction opposite to the photoreceptors. The subsequent emergence of physiological methods has made it possible to examine the functions of the neurons in the retina.

The first to do so was Haldan Keffer Hartline, who developed procedures that enabled him to record the electrical activity of individual retinal ganglion cells (3). Doing so, he discovered three classes of retinal ganglion cells: “ON” cells that discharged vigorously when the retina was illuminated, “OFF” cells that discharged when the light was turned off, and ON/OFF cells that responded transiently to both the onset and the termination of light. He also established that each cell is sensitive to only a small area of illumination on the retinal surface, a region called the receptive field of the cell. Hartline received the Nobel Prize for these discoveries in 1967. Subsequently, Steven Kuffler discovered in the cat, as did Horace Barlow in the frog, that the receptive field of each ganglion cell is actually composed of two regions that are concentrically arranged: an excitatory center area and an antagonistic surround region (4, 5). Stimulation of the center with a small spot elicited a vigorous response, whereas a larger spot that impinged also on the surround produced an attenuated response. Stimulation of the surround alone with an annulus produced a weak response of the opposite polarity. The ON/OFF cells gave vigorous transient responses to both the onset and the termination of light when confined to the center of their receptive fields; in these cells, the responses were also attenuated when the size of the stimulus was increased. Similar results were obtained subsequently in many species suggesting that the ON, OFF, and ON/OFF cells of the retina and their antagonistic center-surround organization form a basic ground plan for the visual systems of all vertebrates (6–9).
The intracellular recording studies have also revealed that photoreceptors, horizontal cells, and bipolar cells produce only graded potentials. Center-surround organization appears at the level of the bipolar cell (11). Action potentials are first seen in some amacrine cells and are produced by all ganglion cells. The axons of the ganglion cells project to a number of different nuclei in the brain, the largest of which, in primates, is the lateral geniculate nucleus (LGN) of the thalamus. This is a structure with several lamina in which the left and right eye inputs are segregated. In addition, there is a propensity for the various retinal ganglion cell types to terminate in different layers (6, 8, 9, 17). In a few species, there is a clear or partial segregation of the ON and OFF cells in the LGN (8, 9, 18, 19). Neurons from the LGN project to the visual cortex. Although the receptive field characteristics of LGN neurons are similar to those of retinal ganglion cells, in the cortex several new properties are found (6, 20); the majority of cells in primary visual cortex show selectivity for the orientation of edges, and many cells respond selectively to the direction of motion of these edges.

Anatomical studies have revealed that the ON and OFF bipolar cells are distinct structurally and make connections in the inner retina in different subregions of the inner plexiform layer (IPL), as depicted in Fig. 1B; the OFF bipolar contacts form OFF retinal ganglion cell arbors in sublamina a of the IPL and ON bipolar cells form connections with ON ganglion cells in sublamina b of the IPL (7, 16, 21). The layout of the ON and OFF retinal ganglion cells has been effectively examined in retinal whole mounts, in which the retina is viewed as a flattened preparation. The dendritic arbors of the ON and OFF ganglion cells, once properly labeled, can readily be identified because they come into focus at different depths within the specimen. Using such methods, Heinz Wässle and collaborators discovered that the spacing of the arbors within each of the ON and OFF cell classes, but not between them, is highly orderly (22). This systematic arrangement suggests that the ON and OFF systems provide separate, and probably independent, coverage of the visual field. The synapses bipolar cells make in the inner retina are glutamatergic. Horizontal and amacrine cells come in many different subtypes and use a variety of neurotransmitters that include gamma-aminobutyric acid (GABA), glycine, and acetylcholine. The diversity of horizontal and amacrine cell types appears to decrease in higher mammals in which more complex visual analysis is increasingly relegated to neocortex.

That nature has gone to such complexities to create the ON and OFF systems suggests that great benefits must be reaped for the analysis of visual information. The initial ideas were that the ON system signals the onset of light and the OFF system the terminations of light. As first suggested by Jung (23), another idea that has gained some degree of acceptance was that the ON system gives rise to the perception of brightness and the OFF system to the perception of darkness. A third consideration was advanced by more physiologically minded investigators, who suggested that the ON and OFF systems have evolved to provide for the antagonistic center-surround organization of receptive fields in retinal ganglion cells and in the cortex (24). Two major schemes have been proposed as to how the preganglionic neural elements of the retina connect to the ganglion cells to yield their antagonistic center/surround organization. According to the first, the surround mechanism is supplied by the lateral connections of the horizontal and amacrine cells of the retina. According to the second, the center-surround arrangement of the retinal ganglion cells is produced by convergent connections from ON and OFF bipolar (8, 9, 25). The data gathered during the past few years in primates favor the idea that those cells of the retina that can be unequivocally identified as being ON-center or OFF-center types form separate pathways and do not interact extensively. The surround mecha-

Fig. 1. (A) The basic connections a cone makes with ON and OFF ganglion cells via ON and OFF bipolar cells. The ON bipolar cells have sign inverting synapses as described in the text. (B) The basic connections rods, cones, bipolar cells, horizontal cells, and amacrine cells make in the retina. [Reprinted from Progress in Retinal and Eye Research, Vol 15, Schiller PH, The ON and OFF channels of the mammalian visual system, 173–195, Copyright (1995), with permission from Elsevier]. (C) The responses of an ON and OFF monkey LGN cell before, during, and after the infusion of APB into the eye. APB blocks the ON cell response and has no significant effect on the OFF cell (25). (Reprinted by permission from Macmillan Publishers Ltd: Nature, 297:580–583, copyright 1982.)
nism of these cells is a product of the lateral connections in the retina rather than a product of an interactive connection between the ON and OFF bipolar cells. In the following sections, three lines of evidence will be considered in support of this view, which come from anatomical, physiological, and behavioral studies.

When Ramon y Cajal et al. (2) examined the organization of the retina after the duality of the rod and cone photoreceptors had been established by Schultze (1), the evidence he gathered suggested to him that these two systems form separate pathways to the central nervous system. Subsequent studies have established, however, that, for the most part, where the rods and cones coexist in any region of the retina, their signals converge upon the retinal ganglion cells (26, 27). Furthermore, current studies have shown that, unlike for the cones, the rod system in some mammals—including the cat, monkey, and human—has only ON-type rod bipolar. This has raised some interesting questions about the manner in which the rods might make their connections with the retinal ganglion cells. The nature of this connectivity has been worked out in some detail recently. The rod photoreceptor cells form sign-inverting synapses with the rod ON bipolar cells (28). Examination of the connections of the rods has also established that each rod ON bipolar cell contacts many rod photoreceptors; thus the rods have been said to pool their signals and, by doing so, form relatively large receptive field centers (29). In the inner retina of the cat and probably the monkey, the rod bipolar terminate in the inner portions of the inner plexiform layer, but do not contact ganglion cells directly. Instead, they terminate on amacrine cells, most commonly on the AII type. Each of these amacrine cells in turn makes two major kinds of contacts: one is a gap synaptic junction with ON cone bipolar cells and the other is a glycine/synaptic junction with OFF ganglion cells, as depicted in Fig. 1B (28–30). This arrangement appears to accomplish for the rods in the inner retina what is accomplished for the cones in the outer retina: it turns the single-ended photoreceptor system into a double-ended one. As a result of these connections, under dark-adapted conditions when the cones are unresponsive, the ON ganglion cells are excited by light increment and the OFF ganglion cells by light decrement.

The organization of the receptive fields under light- and dark-adapted conditions is quite different, as was first shown by Barlow et al. (31). This difference, which was subject to considerable incredulity at the time, is now readily understandable. The receptive-field center under dark-adapted conditions is driven by the rods through the bipolar and amacrine cells. The surround mechanism is the product of those portions of bi-tufted horizontal cells that make lateral connections only with the rods (16). As a result of this arrangement, several superimposed receptive fields can be created for any given patch of retina.

**Physiological Studies Using 2-Amino-4-Phosphonobutyrate.** The use of a glutamate neurotransmitter agonist has provided an important line of support for the claim that the ON- and OFF-center ganglion cells form independent pathways to the central nervous system. This substance, 2-amino-4-phosphonobutyrate (APB), was discovered by Slaughter and Miller (32) to act differently on the ON and OFF bipolar cells of the mudpuppy (*Necturus maculosus*) retina. By decreasing membrane conductance, APB produces prolonged hyperpolarization in the ON bipolar cells, as a result of which they become unresponsive to subsequent light stimulation (32, 33).

Current evidence shows that ON bipolar cells have a specific metabotropic glutamate receptor termed mGluR6 that is coupled to a G protein. The activation of this receptor leads to the closing of cGMP-gated cation channels by increasing the rate of cGMP hydrolysis by a G protein-mediated process (34). The mGluR6 receptor responds selectively to 1-2-amino-4-phosphonobutyrate (35). In a remarkable recent study, Masu et al. (36) have succeeded in generating KO mice that lacked mGluR6 expression and hence lacked the ON system. This work further attests to the unique and distinct nature of the ON bipolar cells and the ON system in the mammalian retina except for a transient initial excitatory response, the OFF bipolar cells are largely unaffected by APB. As there is no ready uptake mechanism for this artificial substance, it is effective in small quantities and is broken down slowly. It seems to have little or no direct effect on the synaptic networks of the inner plexiform layer. **Effect of APB on the responses of single cells in the mammal.** To determine the effect of APB on the mammalian visual system, several investigators have applied this substance to the retina while recording from various visual structures. It became immediately evident that the effects of APB noted in the mudpuppy are similar in the mammalian retina. When APB is administered in appropriate concentrations to the monkey eye, the ON response in retinal ganglion cells is abolished whereas the OFF response is largely unaffected (9, 24, 25, 37). Fig. 1C shows recordings made from an ON and OFF cell in the LGN before, during, and after the infusion of APB into the retina. The ON cell stops responding to the visual stimulus presented in the receptive field of the cell whereas the OFF cell continues to respond.

Having established that APB blocks the ON system in the monkey as it does in the mudpuppy, investigators moved on to determine to what extent the ON and OFF bipolar cells make interactive connections with the retinal ganglion cells to produce their antagonistic center-surround organization. To do so, the center and the surround of receptive fields can be selectively stimulated before and after APB administration. Fig. 2 shows a typical result obtained by recording in the parvocellular LGN of a monkey. The cells shown had color-opponent characteristics and were consequently stimulated with colored spots that preferentially activated the center and the surround mechanism. The center mechanism was activated with a small spot of the appropriate wavelength composition; the surround mechanism was activated briefly both when the center was stimulated and during the off cycle using a large spot of a different wavelength composition appropriate for the surround. The inhibitory effect of the surround stimulation is evident for both the ON and the OFF cell under normal conditions. Following administration of APB, the responses of the ON cell are eliminated whereas the responses of the OFF cell, including the center-surround antagonism produced by the stimulus that activated the surround mechanism, are mostly unaffected. These findings support the idea that the center-surround organization of retinal ganglion cells and LGN cells is not a product of ON and OFF cell interactions, but rather a product of the lateral networks of the retina that involve the horizontal and perhaps the amacrine cells. Thus the model of retinal organization these findings support is that the ON- and OFF-center ganglion cells, most of which send their axons to the LGN, form separate pathways (25, 37, 38). Also favoring this model is an elegant study by Mangel and Miller (39) in which hyperpolarizing current, injected intracellularly into rabbit horizontal cells, produced a decrease in the firing rate of ON ganglion cells and an increase in OFF ganglion cells.

**Effects of APB on ON/OFF cells.** The ON/OFF cells that respond transiently to both light increment and light decrement comprise the third category of retinal ganglion cells that had been identified by Hartline (3); these cells are thought to arise as a result of convergent input from the ON and OFF bipolar cells onto individual retinal ganglion cells where the dendritic arbors of the ON/OFF ganglion cell are bistratified. In the primate retina, the ON/OFF retinal ganglion cells project extensively to the superior colliculus (40). In many species, such cells also project into the geniculostriate system (6, 41). Retinal administration of APB eliminates the response to light increment but not to light decrement in collicular cells (42).

**Effects of APB on single cells in area V1.** The retinal input through the LGN to primary visual cortex, commonly referred to as V1, is transformed in a number of ways, as already noted, yielding neurons that are orientation and direction-specific (6, 20). Many of the neurons receive convergent input from the left and right eyes. V1 neurons are most effectively activated by edges with specific orientations. The characteristics of V1 neurons were first revealed by Hubel and Wiesel (20), who received the Nobel Prize in 1981.
Two major classes of cells they have identified in area V1 are the simple and complex cells. Simple cells have receptive fields in which there are spatially distinct ON and OFF regions, whereas in complex cells the ON and OFF regions overlap spatially (6, 20, 43). When a properly oriented bar is swept across the receptive field of V1 complex cells, a response is elicited by both the light and dark edges of the bar as it sweeps across the receptive field. This is shown in Fig. S1A. When the ON channel is inactivated by APB infusion into the eye, the light edge response is eliminated but the dark edge response remains. This indicates that the light edge response is caused by the input from the ON system and the dark edge response to a result of the input from the OFF system.

It has been proposed that the direction and orientation specificity of V1 neurons is a product of the interaction between the ON and OFF systems. An alternative hypothesis proposed was that inhibitory intracortical circuitry achieves these attributes in V1 cells (6, 20, 43). Inactivation of the ON channel with APB shows that direction specificity and orientation selectivity remain unaffected. Fig. S1B shows the responses of a complex cell in monkey V1 that under normal conditions responds preferentially to downward motion. After APB infusion, the leading light edge response is blocked but the directional selectivity of the cell persists. In Fig. S1C, orientation tuning curves are shown before and after APB infusion. The orientation tuning function is unaffected by the APB block. These findings indicate that orientation and direction specificities are a product of intracortical circuitry rather than interactions between the ON and OFF channels. That retinal APB infusion does not significantly affect orientation and direction specificities in area V1 has also been established in the cat by Sherk and Horton (44).

Behavioral Studies of ON and OFF Channels Using APB. Further insights into the role of the ON and OFF channels in vision come from behavioral studies in which the visual capacities of animals were assessed before and after the ON channel was blocked with APB. In monkeys, the most notable deficit observed under light-adapted conditions was for the detection of stimulus spots made visible by virtue of increases in light energy; that is, spots that are perceived as brighter than the background (9, 24, 45, 46). There was little or no deficit in the detection of spots that were darker than the background. Examples of this are shown in Fig. 3, in which both percent correct and reaction-time data are presented. Following APB administration the percent correct responses for the detection of light increments decreases dramatically, which is accompanied by large increases in the response latencies; performance with stimuli seen by virtue of light decrement is unaffected. These observations fit with the idea that the ON channel is sensitive to light incremental stimuli and signals lightness, whereas the OFF channel is sensitive to light decrement and signals darkness—an idea, as already noted, that had been advanced earlier by Jung (23).

Behavioral studies in monkeys have also shown that, under dark-adapted conditions, when only the rods are functional, APB blocks the detection of stimuli seen by virtue of either light increment or light decrement; in other words, the rod system is blocked in its entirety and, consequently, the animal becomes night-blind (9, 47). These findings provide additional support for the claim that the rod bipolars in the primate are all ON types.

Midget and Parasol Channels

Anatomy and Physiology of Midget and Parasol Systems. In 1966, Enroth-Cugell and Robson (48) published an influential article showing that, in the cat, they distinguished three distinct classes of retinal ganglion cells, which they called the X, Y, and W. Subsequently, it has been found that similar subclasses of retinal ganglion cells exist in most mammalian species (49, 50). In the primate, two of these classes were named the midget and parasol systems. The ganglion cells of the midget system, as the name implies, are quite small. The parasol cells, by contrast, are much larger, with their dendritic arbors and receptive field diameters being approximately three times greater than the midget cells. The axons of the parasol ganglion cells are larger and have faster conduction velocities than do the axons of the midget cells. Fig. 4A provides a cross-sectional view of the midget and parasol cells as created by Polynak (51). Fig. 4B shows the dendritic arbor arrangement of these cells as seen in a whole-mount preparation by Watanabe and Rodieck (52).

The midget and parasol cells come in both ON and OFF subvarieties. The input to the receptive field center of the midget cells of the monkey is composed of a single cone in the central retina. Thus, a single cone will give rise to both an ON and OFF bipolar cell, as shown in Fig. 1A and B. By contrast, the receptive field center of the parasol cells is comprised of several cones that are not segregated according to type (16, 50). The receptive field sizes of these two classes of cells are quite different as are their inputs. The excitatory center of the midget cells in central retina is comprised of a single cone, thereby rendering them color-selective. The excitatory center of the parasol ganglion cell receptive fields is comprised of several cones, as is the surround, indicating that these cells cannot convey information about color. The parasol cells, however, are not insensitive to stimu-
The midget and parasol systems have their own set of ON and OFF bipolars. This arrangement in the midget system (53)–(57) is organized in a pure color-opponent fashion. Thus, the midget cell, which is relatively large in diameter, as are their dendritic arbors, and they respond to visual stimuli in a transient fashion; midget cells, by contrast, produce a rather sustained response.

The ability to experience different colors lies within the domain of the midget system (54–58). Until recently it was believed that the midget system is organized in a pure color-opponent fashion. Thus it was assumed that any given midget cell whose receptive field is centered on a long-wavelength cone, has a surround that is driven by middle-wavelength cones. Serious questions have been raised during the past few years about the validity of this inference. It has been shown that the horizontal cells of the retina, even for the midget system, are “promiscuous”: they make contact with all cones within the area they sample (16). If color opponency is the product of interaction between the center and the surround mechanism created by the horizontal cells, it appears that the opponency is not pure; it does not arise by pitting red cones against green ones (red/green opponency) and blue cones against red plus green ones (blue/yellow opponency), but by pitting individual short-, middle-, and long-wavelength cones forming the center mechanism against all cones that feed into the surround mechanism. That this is a computationally viable alternative has been established by Lennie et al. (59). It must be recognized, however, that possible interconnections in the inner retina could provide a clear color-opponent system. The midget and parasol cells of the retina project predominantly to the LGN in the trichromatic primate, where the midget cells make connections within the parvo-cellular layers and the parasol cells within the magnocellular layers. In turn, the cells in these two sets of layers project to the striate cortex, where they terminate predominantly in layers 4a and 4β, respectively. Within the striate cortex, some cells, after a cascade of connections, receive a convergent input from these two systems (60). Some of the cortical cells, however, are driven exclusively by one or the other system, although there is commonly a convergence of the ON and OFF subtypes, as has already been noted. Recent studies of the connections from the striate cortex to extrastriate...
regions have shown that the input to area MT is dominated by the parasol system, whereas the input to area V4 is mixed (61, 62).

The ratio of the midget and parasol cells changes notably as a function of eccentricity. In the center of the fovea (sometimes called the foveola), there are virtually no parasol cells. Near the fovea, the midget cells outnumber the parasol cells by approximately eight to one. This ratio changes gradually until, in the far peripheral representation, they become equally represented (63). This is consistent with the notion that the midget system is clearly reflected in the LGN. In central representation, out to approximately 18°, the LGN most commonly has six layers. The dorsal four layers are called parvocellular and contain medium-sized cells. These layers receive input from the retinal midget cells (64, 65). The ventral two layers are called magnocellular and contain large cells that receive input from the retinal parasol cells. Beyond 18° of the visual field representation in the LGN, the layers are reduced to four: two parvocellular and two magnocellular ones. Thus, in central representation, the midget cells are far more numerous than the parasol cells, whereas in peripheral representation, they are equal in number (66).

**Behavioral Studies Examining Functions of Midget and Parasol Systems.** A variety of behavioral experiments have been carried out that examined the functions of the midget and parasol systems. Some of these experiments have used visual stimulus conditions that selectively activated the midget or parasol systems (50, 66–68). Another set of experiments blocked the midget or parasol systems by making selective lesions in the parvocellular and magnocellular portions of the LGN (49, 50, 67).

To assess the role of these two systems in vision, monkeys had been trained to perform a variety of visual tasks using detection and discrimination tasks. Each trial began with a fixation spot appearing in the center of a monitor the monkey faced. Upon fixation, as determined by monitoring the monkeys’ eye movements, either a single stimulus appeared (the detection paradigm) or an array of stimuli was presented, one of which, the target, was different from the others, called distractors (i.e., oddity task). The monkey was rewarded for making a saccadic eye movement directly to the target. The contrast, size, color, and/or shape of the target or the distractors was systematically varied. The target was presented in intact regions of the visual field or in regions where the midget or the parasol system was blocked (50, 67). Fig. S2 shows data obtained from a monkey that assessed color, texture, and pattern processing. Fig. S24 shows data obtained in a color discrimination task using the oddity task. The target in this case had a different color from that of the isoluminant distractors of a different color. The data show that, after a midget system block, the monkey was no longer able to make color discriminations. Conversely, the parasol system block did not have much of an effect on color discrimination. These findings establish the fact that color processing is accomplished by the midget system. Fig. S2B shows the texture detection task. A single target appeared on a textured background with the target consisting of a small square area within which the diagonal lines were reversed relative to the background. Blocking the midget system brought performance to chance, whereas blocking the parasol system had no effect on texture detection. Fig. S2C shows a pattern discrimination task; the target is different from the distractors by having checkerboards of a lower spatial frequency. The data show that a midget system block eliminates the ability of the monkey to discriminate fine differences in the perception of patterns whereas a parasol system block has no significant effect on pattern perception. In contrast with these dramatic effects, when monkeys were tested for brightness discrimination, it was found that this capacity was unaffected by a midget or parasol block, indicating that both these systems can process this capacity.

Fig. S3 shows data obtained on stereoscopic depth perception, motion detection, and flicker detection. Stereoscopic depth perception has been studied extensively using random-dot stereograms as initially developed by Julesz (68, 69). To study this in monkeys, the monkeys were trained to look through a stereoscope. A small region in the stereogram was arranged to appear in depth by virtue of the disparity introduced. A saccadic eye movement made to this region was rewarded. The top section of Fig. S3 shows data obtained using this procedure. Following a midget system block, the monkeys’ ability to perform on this task was devastated. The deficit was complete at the lowest disparity. There was no deficit when the parasol system was blocked. These findings suggest that the midget system plays a central role in stereopsis, especially at high spatial frequencies and low disparities. The parasol system, however, seems to be able to contribute to this mechanism at low spatial frequencies and high disparities.

To study motion, the display consisted of an array of randomly placed small dots. On each trial in a small region of the visual field, the dots were set in motion. A saccadic eye movement made to that location was rewarded. The contrast of the dots was systematically varied. The data in the central section of Fig. S3 show that a midget system block had no effect on motion discrimination whereas the block of the parasol system created a major deficit. In another study, depth analysis based on motion parallax was examined, which showed that the parasol system plays a central role in processing this information (68).

The bottom section of Fig. S3 shows data obtained when the task was to discriminate flicker from nonflicker. To do so, an array of light-emitting diodes (LEDs) was used, the flicker rate of which could be varied over an extensive range. The data show that, when the parasol system is blocked, a major deficit arises in flicker perception. These data establish that the parasol system plays a central role in temporal processing that includes motion and flicker.

Based on these data, we can conclude that the midget system plays a central role in color, pattern, texture, and stereoscopic depth perception whereas the parasol system plays a central role in motion perception, flicker perception, and depth processing based on motion parallax. Both systems contribute to brightness perception. As a result of this work, we believe the midget and parasol systems have evolved to extend the range over which visual information can be effectively processed. The midget system extends it in the high spatial frequency and wavelength domains whereas the parasol system extends it in the temporal domain.

**Accessory Optic System.** The accessory optic system (AOS) originates in the retina. Its ganglion cells project to three target nuclei in the anterior portion of the midbrain: the dorsal, medial, and lateral terminal nuclei (70–72). The morphology of retinal ganglion cells projecting to the terminal nuclei was first studied in the pigeon by Karten and collaborators in the 1970s (72–74). They showed that these were the displaced ganglion cells of Dogiel whose distribution on the retinal surface was remarkably orderly. In the rabbit, which has approximately 350,000 ganglion cells, there are approximately 6,000 to 7,000 directionally selective cells of Dogiel that project to the nuclei of the AOS (75).

The responses of direction-specific retinal ganglion cells in the rabbit retina were first studied by Barlow and Levick (76). Based on their work and that of others, it was established that those direction-selective cells of the rabbit retina that respond best to very slow velocities of image motion (0.1–1°/s) are all ON types (75). They have a trilobed spatial distribution of preferred excitatory directions (77). Striking about these observations was the discovery that the three axes of direction selectivity correspond to the planes of three principal axes of the semicircular canals. The neurons in the terminal nuclei of the rabbit to which the displaced ON-type direction selective cells of Dogiel project have similar properties but have much larger receptive fields. The preferred direction of cells in the dorsal terminal nucleus was found to be from posterior to anterior in the horizontal plane. Cells in the medial and lateral terminal nuclei had upward or downward excitatory directions, both with a posterior component. Inhibition plays a prominent role in the AOS as approximately 50% of the cells have positive glutamic acid decarboxylase reactions (78, 79). The terminal nuclei project to the dorsal cap of...
Kooy of the inferior olive (80, 81), which gives rise to climbing fibers projecting to the flocculonodular lobe of the cerebellum. The dorsal cap of the inferior olive also receives a projection from the nucleus of the optic tract, which has been studied by Collewijn and others (82, 83). This structure, like the terminal nuclei, receives input from direction selective cells of the retina, but of a different class that gives both ON and OFF responses and responds best to higher velocities of stimulus motion. Electrical stimulation of these regions elicits nystagmic eye movements akin to those obtained during optokinetic nystagmus, and lesions produce deficits in the tracking of moving stimuli. As in the rabbit, the retinal direction selective cells projecting to the terminal nuclei are all ON types, it is possible to assess the role of these cells in the generation of optokinetic nystagmus by applying APB to the retina while the animal is exposed to slowly moving vertical stripes. When this was done by Knapp et al. (84), they found that the optokinetic nystagmus was abolished. This finding provided additional support for the idea that the ON direction-selective cells of the retina provide the essential input, via the terminal nuclei, for the generation of tracking eye movements for large stimulus constellations. This curious arrangement of having only ON-type cells that project into the AOS in the rabbit is not found in all species. Although in the turtle and zebrafish, similar results have been obtained (85, 86), this was not the case in the cat or monkey. In these species, only mild effects of APB were found on OKN, which was restricted to high spatiotemporal frequencies (84). This suggests that in these species both the ON and OFF channels contribute to the OKN. In the goldfish, APB also failed to abolish the OKN (87); it was subsequently discovered, however, that in teleosts there are two mechanisms of ON-bipolar generation, one of which is not sensitive to APB (88).

On the basis of these observations, a specific function for the AOS emerges as proposed by Simpson et al. (89). The AOS signals self-motion as reflected in the slip of the visual world over the retinal surface. The detection of this slip by the direction- and velocity-selective cells of the AOS triggers a chain of activity through the pathways of the AOS that produces corrective eye movements, resulting in the stabilization of the retinal image. At higher velocities such stabilization is typically accomplished by the vestibular system. Hence, the AOS nuclei and the vestibular apparatus form two complementary systems geared toward the detection of self-motion and the appropriate corrective action for image stabilization, thereby allowing for the rapid and accurate analysis of objects that appear in central vision.

Other Parallel Channels Originating in the Retina

In addition to the systems discussed so far, several others have been found to originate in the retina. These include the so-called W system, directionally selective cells other than those that project to the terminal nuclei, the pupillary system, a small complement of cells that project to the hypothalamus, and the so-called koniocellular (K) system. The W-type cells of the retina, described in the cat and monkey by a number of investigators, appear to be a “grab-bag” category that actually consists of several subtypes and seems to include the ON/OFF retinal ganglion cells (90). Anatomically, these cells are likely to be of the δ and γ types (16). Many of these cells come in both ON and OFF subvarieties and, as already noted, project extensively to the superior colliculus and also to the pretectal nuclei. Prominent among the pretectal nuclei is the nucleus of the optic tract that receives input from those direction-selective retinal ganglion cells that respond to higher velocities and come in both ON and OFF subtypes. Another visually driven structure in the pretectum is the olivary nucleus, which is involved in the generation of the pupillary reflex. As studied in the rat and rabbit (42), it appears that the cells of the olivary pretectal nuclei are all excited, in a tonic fashion, to light increment, suggesting that they are exclusively of the ON type. This is supported by the finding that, in the rabbit, retinal administration of APB eliminates responsiveness to light in the olivary pretectal nucleus. However, when the optokinetic reflex was examined in rabbit and monkey following APB blockade of the ON system in the retina, the reflex was only mildly impaired. This suggests that other pathways and the OFF system can make a contribution to light activation of the ciliary muscles (42).

Yet another class of retinal ganglion cells that has been identified are the K cells that express oCAM kinase/calbindin. This system has been extensively studied; several reviews describe it in detail (91–98). Many of the K ganglion cells have bistratified dendritic arbors, as a result of which they receive both ON and OFF inputs from bipolar cells. Some of them are driven by blue cones. A subgroup of these cells project to the intralaminar layers of the LGN, from which the projections are predominantly to the upper layers of area V1 (91–93, 95).

On the basis of the foregoing it is evident that, from the single layer of photoreceptors, a series of parallel pathways are created by the stunningly complex and elaborate circuitry of the retina. There are many different retinal ganglion cells that project selectively to a variety of central nuclei and are involved in different aspects of visual information processing. Furthermore, in some of these systems, the same set of retinal ganglion cells can carry several kinds of different messages. For example, the midget cells, when excited in the daytime by the cones, can carry information about both color and luminance; at night, when they are driven by the rods, the receptive fields of these same cells take on a different configuration and convey messages about only luminance. This arrangement renders these cells multifunctional.
