Primate Retina: Duplex Function of Dark-Adapted Ganglion Cells

Abstract. *Certain ganglion cells from the central region of dark-adapted retina of the rhesus monkey respond to stimulation of both rod and cone receptors. With dim stimuli the function of these ganglion cells is determined entirely by the rods; with brighter stimuli that affect both dark-adapted rods and cones, little evidence of rod function is detectable because a cone mechanism appears to determine both the latency and frequency of ganglion-cell firing.*

A Purkinje shift, so characteristic of the function of duplex retina, has been shown to occur at single ganglion cells of a number of vertebrates (*1*) other than primates. In virtually all these studies cone activity has been induced by adapting the retina to light and thereby preferentially reducing the sensitivity of the rods. Such results have shown that both rods and cones can transmit their signals to the central nervous system by way of identical cells, the rods in the dark-adapted state and the cones in the light-adapted state.

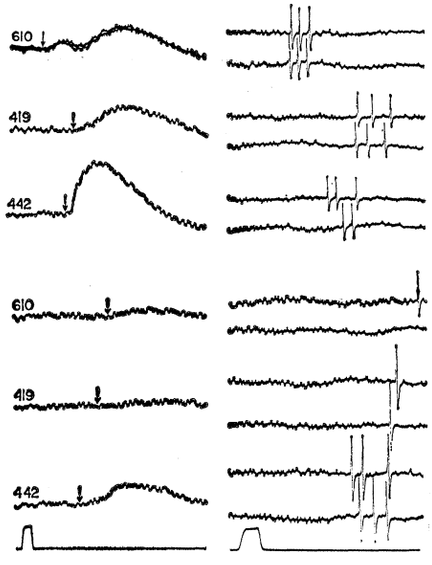

Fig. 1. Action potentials of a single ganglion cell (right) and the electroretinogram (left). The stimuli at wavelengths of 610 and 419 nm are approximately equal as regards scotopic vision, whereas the stimulus at 442 nm is greater. In the upper group, stimuli are suprathreshold for the cones, as evidenced by the early photopic component in the electroretinogram obtained with stimulation at 610 nm. In the lower group, the stimuli are below cone threshold. The lowest traces are the responses of vacuum-tube photocell to the 10-msec light pulse. The arrows indicate when the earliest spike occurs relative to the electroretinogram. The vertical calibration signifies 0.05 mv for the electroretinogram and 1 mv for the spikes.

In this report experiments are described which demonstrate that ganglion cells from the central retinas of rhesus monkeys also respond to stimulation of both rods and cones. Even when both receptor systems are fully dark-adapted, the cones maintain a strong influence on the ganglion cell as long as the stimulus is sufficient for the cones.

Responses from single ganglion cells were obtained from monkeys anesthetized with nembutal. Glass micropipettes, filled with 3*M* potassium chloride, were guided with the aid of a microscope through a small scleral hole near the limbus of the eye into the vitreal cavity to the central retina. The cornea was protected by a contact lens and the pupil was widely dilated with cyclopentolate hydrochloride so that the fundus could be observed with an ophthalmoscope. The eye was stimulated in a Maxwellian view aligned along the visual axis and subtending 83° of visual angle. The light source was a well-regulated 1000-watt, high-pressure xenon arc lamp from which parallel rays could be filtered by relatively monochromatic interference and neutral-density filters. The energies of the stimuli were measured by a standardized thermopile and galvanometer. Each stimulus was of 10-msec duration and was presented every 2 seconds to an eye adapted to darkness for 30 minutes or longer. Successive responses to the flash energies used did not differ appreciably from each other, indicating that the state of adaptation to darkness was restored in the 2-second intervals between flashes. The state of retinal adaptation was also evaluated by the electroretinogram, recorded by the same electrode within the vitreous. A silver chloride reference electrode was located within Tenon's capsule behind the eye.

Both the spectral sensitivity (*2*) and the action spectrum for obtaining threshold electroretinograms in response to stimuli subtending large visual angles (*3*) in the dark-adapted rhesus monkey closely resemble human scotopic vision. For this reason the energies of differently colored lights which have equal effects on the rod receptors can be determined by equating them for producing identical effects on either human scotopic vision or the electroretinogram from the dark-adapted monkey. Ganglion cells which mediate only rod vision should behave identically to lights balanced for scotopic vision. Differences indicate the intrusion of receptors which do not contain rhodopsin and which are, presumably, cones.

Ganglion cells, selected because they respond relatively rapidly with a spike

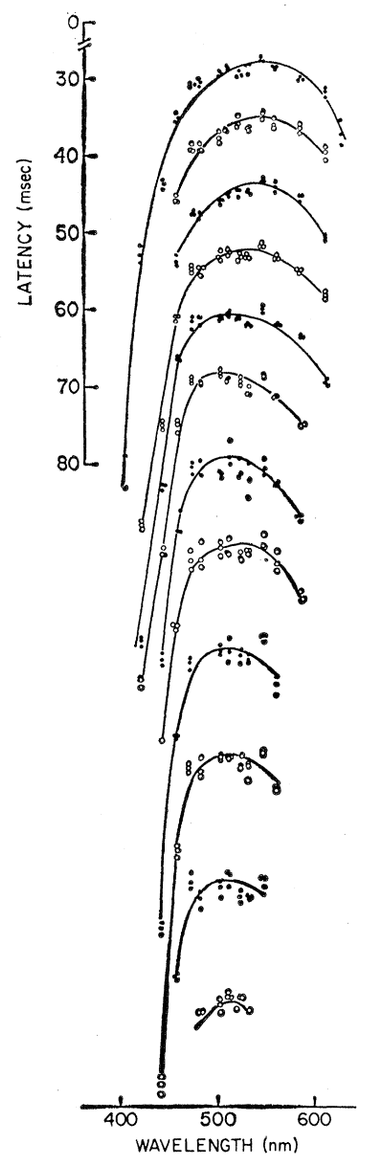

Fig. 2. Latency of initial discharge of a ganglion cell after stimulation with light of different wavelengths but of approximately equal energies. The energy was decreased by a factor of 2 successively from top to bottom. The upper group of points correspond to the ordinate scale. The others have been shifted 5 msec successively from each other along the ordinate.

discharge to these brief light pulses, respond in a characteristic manner to stimuli balanced for scotopic vision. If the stimuli are above the threshold for the cones, as evidenced both by the presence of color when they are observed by human subjects through the same optical system and by the presence of photopic components in the electroretinogram of the monkey, light of long wavelength is always more effective in stimulating the ganglion cell than the equivalent light of short wavelength (Fig. 1). As the stimuli begin to fall below cone thresholds, as evidenced both by the fading of color in humans and by the presence of scotopic components in the electroretinograms, lights balanced for scotopic vision begin to produce identical effects on the ganglion cell (Fig. 1). The shift from cone to rod action takes place when the retinal stimulus is approximately 10^6 quanta deg^{-2} $pulse^{-1}$ at 558 nm (nm $= 10^{-9}$ meter).

The latency of the response is an aspect of ganglion cell function which demonstrates this behavior. Figure 2 shows the latency of a single ganglion cell to monochromatic stimuli, the energies and scotopic effectiveness of which are known. With relatively bright stimuli, the latency is much shorter in response to light of long wavelength than to light of short wavelength, the lights being of equal scotopic strength. At this point the energies required to produce the same response latency at different wavelengths resemble the spectral sensitivity of peripheral cone vision in man (*4*). As the energies of the stimuli are reduced, the peaks of these curves shift to the light of shorter wavelength and the light of long wavelength progressively ceases to elicit any responses at all. With the dimmest stimuli, latency is determined wholly by the scotopic strength of the light. The pattern illustrates a Purkinje shift of single ganglion cells that occurs without light-adapting the rods; a relatively similar pattern is observed if spike frequency is plotted.

It is interesting that, when a stimulus is suprathreshold for the cones, the action spectrum for eliciting either a constant latency or frequency of firing in a ganglion cell reflects cone function, even though the dark-adapted rod receptors are strongly excited. The large amplitude of the scotopic component of the electroretinogram demonstrates the strong rod activation. Somewhere between the ganglion cell and the electroretinogram, the rod signal is lost when stimuli are relatively bright. The brief burst of ganglion-cell activity, which appears before most of the electroretinograms with such stimuli, suggests that the cell is not only excited but subsequently inhibited rapidly so that only the fastest signal to traverse the retina can produce excitation. After bright stimulation this always reflects cone function. The inhibitory surround of ganglion cells demonstrated in a number of vertebrates (*5*) and shown to disappear after the rods begin to determine threshold (*6*) could be responsible.

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References and Notes

1. R. Granit, *Acta Physiol. Scand.* **7**, 216 (1944); H. B. Barlow, R. Fitzhugh, S. W. Kuffler, *J. Physiol.* **137**, 327 (1957); K. O. Donner and W. A. H. Rushton, *ibid.* **149**, 303 (1959); R. M. Chapman, *J. Opt. Soc. Am.* **51**, 1102 (1961).
2. D. S. Blough and A. M. Schrier, *Science* **139**, 493 (1963).
3. P. Gouras, *J. Opt. Soc. Am.* **55**, 86 (1965).
4. W. D. Wright, *Researches on Normal and Defective Colour Vision* (Kimpton, London, 1946); G. Wald, *Science* **101**, 653 (1945).
5. S. W. Kuffler, *J. Neurophysiol.* **16**, 37 (1953); H. B. Barlow, *J. Physiol.* **119**, 69 (1953); D. H. Hubel and T. N. Wiesel, *ibid.* **154**, 572 (1960); H. G. Wagner, E. F. MacNichol, Jr., M. L. Wohlbarsht, *J. Opt. Soc. Am.* **53**, 55 (1963).
6. H. B. Barlow, R. Fitzhugh, S. W. Kuffler, *J. Physiol.* **137**, 338 (1957).
7. I thank K. Link and R. D. Gunkel for assistance.

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Underwater Visual Discrimination by the California Sea Lion

Abstract. *Two captive sea lions (*Zalophus californianus*) presented with a series of size-discrimination tasks showed preferences for the smaller of two targets and gave virtually errorless performances despite changes in the form and relative size of the targets. Further tests revealed that they were capable of discriminating a size-difference ratio as small as 1.06 : 1.*

Seals and sea lions emit series of short pulses while apparently searching for underwater objects—usually food (*1*). These pulses appear to be similar in many ways to the sonar clicks of the porpoise as described by Kellogg (*2*) and are considered by Poulter (*3*) to be ideally suited for the echo detection of objects under water. If seals and sea lions do have a superior sonar system, then a question arises as to the role that underwater vision plays in the abilities of these animals to navigate and find food. Although anatomical and physiological evidence suggests that most pinnipeds have good underwater vision (*4*), there have been no previous experiments dealing with the sea lion's visually guided behavior in an underwater environment. We have, therefore, studied the ability of sea lions to differentiate among targets of various sizes while monitoring their underwater sounds.

All testing was conducted in an oval tank constructed of redwood and measuring 4.57 m by 9.14 m and 1.83 m deep (Fig. 1). The interior of the tank was painted white; during testing it was filled with 81.8 kiloliters of fresh water, and animals could be observed and photographed by means of six windows spaced around the perimeter of the tank. A hydrophone (*5*) was usually available for recording and monitoring underwater sound signals.

We used two female California sea lions (*Zalophus californianus*), which, at the time of their arrival at our laboratory (26 February 1964) had been in captivity for approximately 3 weeks; each weighed 25 kg. They were approximately 17 to 20 months old when training was initiated. The sea lions were usually deprived of food for 22 hours before a test session.

The experimenter worked from behind an opaque screen which was set out 15.2 cm from the dock area and extended down to the water line (see Fig. 1). Targets were presented simultaneously so that they projected below the opaque screen and were at least 38 cm below water level. At the beginning of a trial, a stimulus panel located behind the opaque screen was lowered to the water level. Attached to the side of the stimulus panel facing the experimenter were two rods, 114 cm in length and 0.64 cm in diameter. The targets were cut from 20-gauge sheet metal and were attached to the lower portion of each rod by means of set screws. Deflection of either rod activated a microswitch and produced a light signal behind the stimulus panel. A perpendicular divider of 3.8-cm pine projected 45 cm downward from the water level and 45.7 cm outward from the opaque screen, thus lying between the targets and preventing the animals from moving laterally from one target to the other. The distance between the centers of any two targets was 57.2 cm (Fig. 2).

Prior to formal testing both animals were trained to push with their noses