

The Eel Retina

Receptor Classes and Spectral Mechanisms

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ABSTRACT Light and electron microscopy revealed that there are both rods and cones in the retina of the eel *Anguilla rostrata*. The rods predominate with a rod to cone ratio of 150:1. The spectral sensitivity of the dark-adapted eyecup ERG had a peak at about 520 nm and was well fit by a vitamin A₂ nomogram pigment with a λ_{\max} = 520 nm. This agrees with the eel photopigment measurements of other investigators. This result implies that a single spectral mechanism—the rods—provides the input for the dark-adapted ERG. The spectral sensitivity of the ERG to flicker in the light-adapted eyecup preparation was shifted to longer wavelengths; it peaked at around 550 nm. However, there was evidence that this technique might not have completely eliminated rod intrusion. Rod responses were abolished in a bleached isolated retina preparation, in which it was shown that there were two classes of cone-like mechanisms, one with λ_{\max} of 550 nm and the other with λ_{\max} of <450 nm. Ganglion cell recording provided preliminary evidence for opponent-color processing. Horizontal cells were only of the L type with both rod and cone inputs.

INTRODUCTION

This and the accompanying paper report on the visual physiology of the retina of the eel *Anguilla rostrata*. *Anguillae* are especially interesting because of their unusual life-cycle. They are born in the mid-Atlantic Ocean, migrate to coastal and inland waters where they spend the greater part of their lives, and then migrate back to the mid-ocean to spawn (Bertin, 1956). The change in the eels before the migration is one of the most dramatic of all biological metamorphoses. The eels mature sexually before the spawning migration. This maturation is accompanied by a loss of skin pigmentation (yellow → silver skin) and a marked hypertrophy of the eyes. These changes are probably under hormonal control (Fontaine, 1975). The hypertrophy of the eyes is accompanied by an enlargement in the size of the rod photoreceptors (Carlisle and Denton, 1959). Another change which occurs before the spawning migration is a dramatic shift in the absorbance spectrum of the visual pigment of *Anguilla*. It changes from predominantly a vitamin A₂ pigment with peak absorption at 525 nm to a vitamin A₁ pigment with peak absorption at 480 nm. This change involves the

opsin as well as the chromophore (Carlisle and Denton, 1959; Dartnall, 1962; Beatty, 1975). All of our work so far has been done on the sexually immature, yellow eels which inhabit coastal waters. We hope it will be possible in the future to do retinal anatomy and electrophysiology on migrating, silver eels.

Another reason why we were attracted to the eel retina was the work of Adrian and Matthews (1927 *a, b*; 1928). They performed classic experiments recording the electrical activity of the optic nerve of the conger eel *Conger vulgaris*. We thought it would be interesting to use contemporary electrophysiological methods on the eel, to update our knowledge of the retinal preparation which had been used at the beginning of modern visual electrophysiology and which had since been somewhat neglected by electrophysiologists.

Several statements by Adrian and Matthews led us to believe that the eel eye would be a particularly good preparation in which to study the spatial summation of photoreceptor signals by ganglion cells. They stated that there were only 10,000 optic nerve fibers (Adrian and Matthews, 1927 *a*). They found that spatial summation affected latency of neural response when the separation between stimuli was as great as 1.2 mm (Adrian and Matthews, 1928). Just as a practical matter, their experimental procedure suggested that the eel eye is extraordinarily robust. They recorded optic fiber activity from intact, excised eel eyes, and they implied that the eye continued to respond well for several hours (Adrian and Matthews, 1927 *a*). It turns out that *Anguilla* is equally robust as *Conger*.

This is the first electrophysiological (ERG and S-potential) study of photoreceptor mechanisms in the eel retina. From our electrophysiological and anatomical studies, we have found that the eel retina is duplex, with many rods and few cones. It resembles in this respect the human peripheral retina. The dark-adapted electroretinogram (ERG) is dominated by a single spectral mechanism (probably the rods), the action spectrum of which fits a Munz-Schwanzara (1967) nomogram for a vitamin A₂ pigment with peak wavelength sensitivity at ~520 nm. This is consistent with optical measurements of the rod visual pigments in the yellow eel (Carlisle and Denton, 1959; Beatty, 1975). From experiments on the ERG of the isolated retina, we have discovered that there are at least two cone-like mechanisms, one with peak sensitivity at 550 nm and the other, a short wavelength cone mechanism, peaking around 450 nm or shorter. This last finding implies that eels have the sensory capacity for color vision.

In the accompanying paper we deal with the characteristics of spatial summation by retinal ganglion cells in the eel retina (Shapley and Gordon, 1978).

MATERIALS AND METHODS

Biological Preparation

Eels *Anguilla rostrata* were obtained from the Eel Pond, Woods Hole, Mass., and kept alive in the Supply Department of the Marine Biological Laboratory in a tank with running seawater. Before an experiment, the eel was dark adapted for 12 h. For a brief period, not exceeding 5 min, the eel was exposed to normal room illumination to enable us to decapitate the animal. This was the most difficult technical procedure in the experiment. After decapitation of the eel, room lights were extinguished, and under

dim red light (Wratten 29 filter in front of a tungsten illuminator), the eye was excised from the animal and opened to form an eyecup. In experiments on the eyecup preparation, the eye was then directly transferred to the experimental chamber inside a light-tight, electrically shielded box. In the isolated retina preparation, the retina was simply peeled from the pigment epithelium and placed receptor-side down on a piece of filter paper moistened with Ringer's solution before placement in the chamber. In the experimental chamber, moistened oxygen was continuously blown over the retina. The room temperature was kept between 18° and 20°C during experiments. Under these conditions, the eel retina remained viable for at least 4 h.

Recording

The ERG was recorded with blunt-tipped micropipettes placed on the vitreal side of the retina and with a silver-silver chloride wire in electrical contact with the scleral surface of the eye. ERG recording was DC and differential, by means of a high input impedance, low-noise, FET differential amplifier designed by J. P. Hervey and Michelangelo Rossetto and built in The Rockefeller University Electronics Shop. The bandwidth of the recording was 0–100 Hz, and the amplifier noise was about 5 μ V p-p.

S potentials were recorded in isolated retinas with the receptor side up. Micropipettes (100–150 M Ω) filled with 4 M potassium acetate were used to record the S potential. Amplification was via a negative-capacitance bridge amplifier designed by Rossetto and built in the Rockefeller University Electronics Shop. The amplified ERG or S potential was led to one channel of a Brush recorder. A second channel was used to record the stimulus timing.

Optical Stimulus

In this study we used a two-channel optical projection system. The sources were 45-W tungsten filament, quartz iodide lamps (GE no. T2½Q, General Electric Co., Wilmington, Mass.). In one channel, a Bausch & Lomb high intensity monochromator (half-amplitude bandwidth set at 15 nm) was interposed (Bausch & Lomb, Inc., Rochester, N.Y.). In the second beam, wavelength control was achieved with interference filters (Optics Technology; half-amplitude bandwidth of 10–15 nm). Retinal illuminance and irradiance was measured by means of a UDT model 40A photometer (United Detector Technology, Inc., Santa Monica, Calif.) with its photocell placed in the plane of the retina. The intensity in each beam was varied by the use of Inconel neutral density filters. Retinal irradiances are given for particular experiments in the figure legends. For these experiments, the stimulus was uniform across the retina. Stimulus onset and offset were controlled by electromagnetic shutters (Uniblitz, Vincent Associates, Rochester, N.Y.) with rise and fall times of less than 1.5 ms.

Experimental Paradigms

In the measurement of dark-adapted wavelength sensitivity of the ERG, we used 0.5-s flashes of monochromatic light presented every 15 s. We started at the shortest wavelength, usually 450 nm, and scanned across the visible spectrum up to 650 nm in 13 or 14 steps, with the same neutral density filter in the beam. Then we repeated the scan but in the reverse direction. The two responses for a given wavelength and intensity could be compared to control for any adaptational effects. The scans were repeated for an ascending series of intensities so as to get an intensity-response function at each stimulus wavelength. The experiments on the isolated retina differed from eyecup experiments in the following way. After the retina was isolated, it was bleached by exposure for 5 min to the unattenuated illumination of a tungsten source with color

temperature of 2,000°K and illuminance of 2×10^3 lm/m² ($\sim 10^{12}$ q/mm² s at 520 nm). Then the retina was dark adapted until thresholds stabilized. After dark adaptation, the wavelength sensitivity was measured as usual.

In measurements of the wavelength sensitivity of horizontal cells in isolated retinas, the typical experimental paradigm was used; the retina was not bleached; the stimuli were presented for 0.1 s or for from 1 to 3 s every 10 s.

Histology

Dark-adapted eel eyes were fixed in Susa's fluid and stained with the Cason's-Mallory-Heidenhain method. Alternatively, eyes were fixed in glutaraldehyde and prepared for electron microscopy by postfixing the tissue in osmium tetroxide and embedding it in Epon. Thicker sections from this material were taken for light microscopy and stained with toluidine blue.

RESULTS

The eel *Anguilla rostrata* is a teleost with a retina which conforms to the pattern for a deep-sea teleost. It has both rods and cones, as can be seen in Fig. 1. The cone nuclei are located high in the outer nuclear layer while the rod nuclei are arranged in columns beneath the cone nuclei. The plane of section in Fig. 1 is nearly parallel to the long axis of the rods and normal to the plane of the retina. The rod:cone ratio was calculated by counting rod nuclei and cone nuclei in a relatively thin section (1–5 μ m) of such an orientation. We then squared the ratio of these two numbers to obtain the ratio of the areal densities of the two receptors. The cone nuclei were about 30% bigger than the rods, so the rod:cone ratio must be multiplied by 1.3 to take into account the greater probability of slicing a cone in a thin section. The rod:cone ratio calculated in this way was 150:1. The rod density was approximately 375,000/mm², and the cone density was 2,500/mm² in the central region of the retina. The rod outer segments appear to be layered (tiered)—a typical specialization of deepsea fish (Duke-Elder, 1958, p. 305). The outer segments of rods and cones in the eel appear also to conform to the typical teleost pattern as can be seen in Fig. 2 (Ramon y Cajal, 1892). This is a low-power electron micrograph of a section cut at roughly the same orientation as in Fig. 1. Thus the plane of section was approximately parallel to the long axis of the rods.

Rod Spectral Sensitivity

The spectral sensitivity of the ERG in the dark-adapted eyecup was measured as an indicator of the wavelength sensitivity of the rods. As described in Materials and Methods, responses from trough of a-wave to peak of b-wave for each wavelength were measured at a number of intensities. From the similarity of waveform of these responses over most of the intensity range, we infer that they most probably arise from a single spectral mechanism. This mechanism may or may not get its input from a single class of photoreceptors. However, since the eel retina has a high rod:cone ratio, since the retina was dark adapted, and since the stimuli covered the whole retina, it is highly likely that the spectral sensitivity determined from ERG responses, like those shown in Fig. 3, was the rod spectral sensitivity. This inference is further supported by

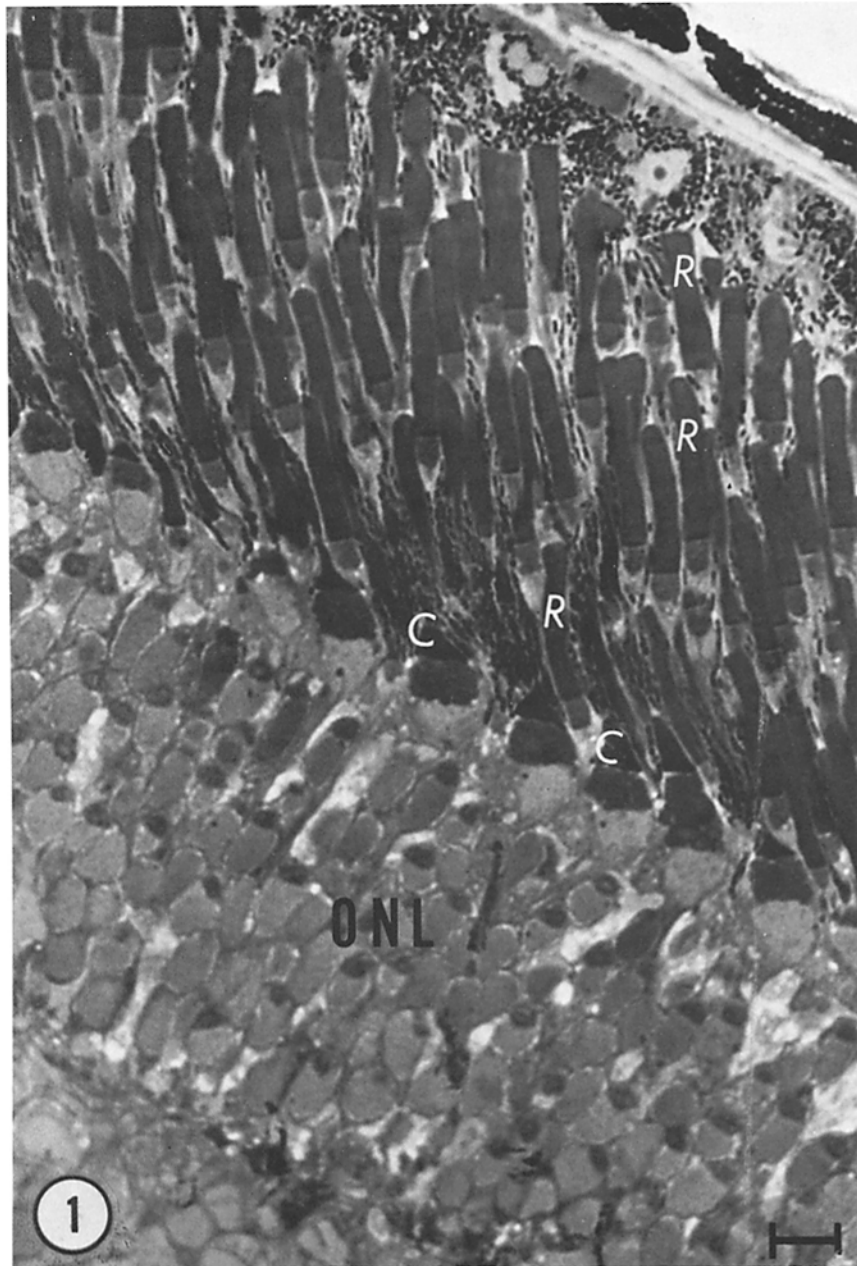


FIGURE 1. Light photomicrograph of an eel retina stained with toluidine blue. The cone nuclei and outer segments form a single row with the nuclei at the distal margin of the outer nuclear layer and a fair amount of intercone spacing. The rods are far more numerous; their nuclei are more proximal than those of the cones and their outer segments are in layers or tiers. Cone outer segments, *C*. Rod outer segments, *R*. Outer nuclear layer, *ONL*. Bar = 5 μ m.



FIGURE 2. Electron photomicrograph of rod and cone outer segments near the inner margin of the photoreceptor layer. The base of the cone outer segment is $\sim 4 \mu\text{m}$.

the similarity of these responses to waveforms produced by rod-driven response mechanisms in other retinas (Granit, 1947; Riggs and Johnson, 1949; Arming-ton, 1974). The following features indicate that these ERG responses were rod driven: the large, sustained b-wave; absence of a marked positive off-response; the long latency-to-peak of the b-wave; and the prolongation of the ERG beyond stimulus offset at high intensities. Since these ERG responses were recorded with a DC amplifier, the prolongation of the ERG responses beyond the termination of the stimulus is particularly well illustrated in our results (Fig. 3, the three lowest responses in each column).

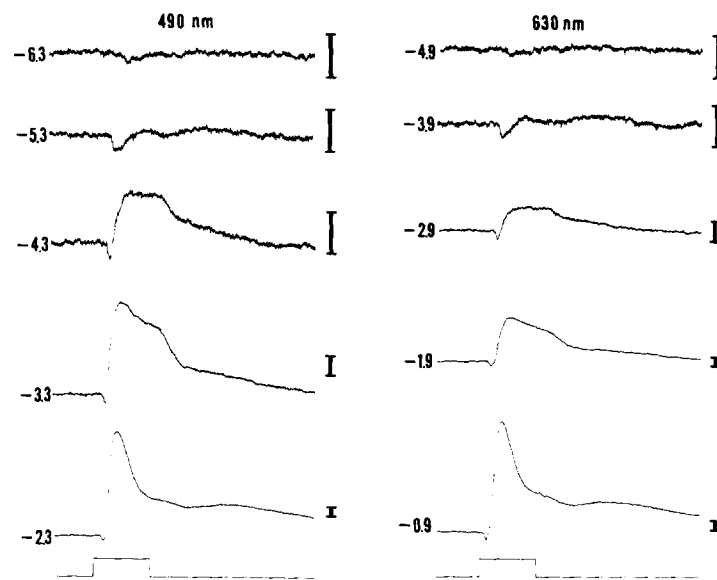


FIGURE 3. ERGs of the dark-adapted eel eyecup to two different wavelengths and a series of intensities. The left column shows responses to 490-nm lights and the right column shows responses to 630-nm lights. The numbers to the left of each record are the stimulus intensities in $\log \mu\text{W}/\text{cm}^2$. The bar to the right of each record represents $50 \mu\text{V}$. Note that the gains used for the various records are not all the same. The stimulus marker under each column is for a flash duration of 0.5 s.

From ERG responses at several intensities, we constructed intensity-response curves. These curves were parallel. A criterion response of $10 \mu\text{V}$ was chosen. Then the reciprocal intensity of the stimulus required to reach this criterion, the sensitivity, was obtained at each wavelength and plotted vs. wavelength as a spectral sensitivity function. Since the intensity response curves are parallel, this function is independent of the criterion chosen. The mean of the spectral sensitivity functions thus produced from three preparations is graphed in Fig. 4. It has been vertically scaled so that peak log relative sensitivity is 2.0. The average peak sensitivity was approximately $(10^{-5} \mu\text{W}/\text{cm}^2)^{-1}$. This implies that at 520 nm the dark-adapted ERG response reached criterion when there were 0.3

quanta per rod per flash incident on the retina. The solid curve is an A_2 nomogram pigment for a λ_{\max} of 520 nm.¹ This is in agreement with the rod pigment measurements of the immature or yellow eel made by Carlisle and Denton (1959) and Beatty (1975). As Beatty (1975) has shown, this pigment is probably a mixture of two visual pigments, a vitamin A_2 and a vitamin A_1 pigment, with the A_2 pigment predominating and determining the wavelength of peak absorption and the overall shape of the absorption function. Our results indicate that the pigment which is most abundant indeed determines the properties of the dark-adapted ERG. The slight decrease in long wavelength

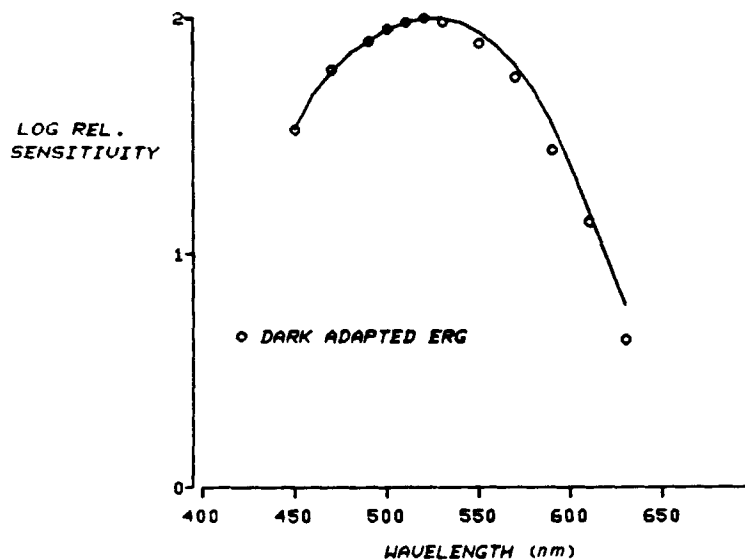


FIGURE 4. Log relative sensitivity as a function of wavelength for the dark-adapted ERG. Open circles represent mean sensitivities for three preparations. The maximum SEM is 0.04 log units. The curve is an A_2 nomogram pigment with a λ_{\max} of 520 nm. The pigment curve shown here, and those shown in subsequent figures, has been appropriately adjusted for plotting on a sensitivity scale based on energy rather than quanta. The pigment curves in all figures have been adjusted vertically for a best fit by eye to the data points.

sensitivity compared to the A_2 pigment curve may be due to the presence of the A_1 pigment.

It might be supposed that the ERG spectral sensitivity could have been broader than the visual pigment density spectrum. Such a result has been obtained in some retinas with high pigment density, and it is usually ascribed to

¹ An electrophysiological action spectrum should in principle be compared with an absorption spectrum rather than a pigment difference spectrum. The latter may be contaminated at short wavelengths by the absorption of photoproducts. In fact, Bridges (1967) has published an estimated absorption spectrum for A_2 pigments. However, this estimated absorption spectrum differs little from the Munz-Schwanzara nomogram based on the difference spectrum, the maximum deviation over the range of our data being 0.13 log units at 450 nm. As it turns out, our data are well fit by the A_2 nomogram, and are almost as well fit by the estimated absorption spectrum of Bridges.

self-screening (cf. Dartnall, 1962). Carlisle and Denton (1959) have measured the pigment density in the yellow eel retina; the mean of their two density values was 0.28. One would therefore not expect self-screening to be an important effect in yellow eels, and our results confirm this expectation.

Cone Spectral Sensitivity

FLICKER The high rod:cone ratio of the eel retina, and the invariance of response waveforms, imply that the eel retina is rod dominated. Therefore, it was necessary to use some of the techniques usually employed to measure the spectral characteristics of cone-driven ERG responses in rod-dominated eyes, e.g., in the human retina (Riggs et al., 1949; Dodt, 1951; Johnson and Cornsweet, 1954). One of the standard approaches we used was fast flicker on a bright background. This technique has been shown to isolate cone responses in other lower vertebrates (Burkhardt, 1966; Gordon, 1967). The background was chosen to be effective in light adapting the rods—in our experiments the background was a 520-nm light at $0.066 \mu\text{W}/\text{cm}^2$ ($\cong 4 \times 10^8$ q/rod s incident on the retina). In other experiments, we found that at this intensity of background the ERG spectral sensitivity curve (measured as before) was broadened with a relative increase in sensitivity at long wavelengths, a result which implies both rod and long wavelength cone contributions. The flicker rate was 10 Hz with a 50% light:dark ratio. The mean spectral sensitivity function obtained from four flicker experiments is shown in Fig. 5. These were determined by taking the

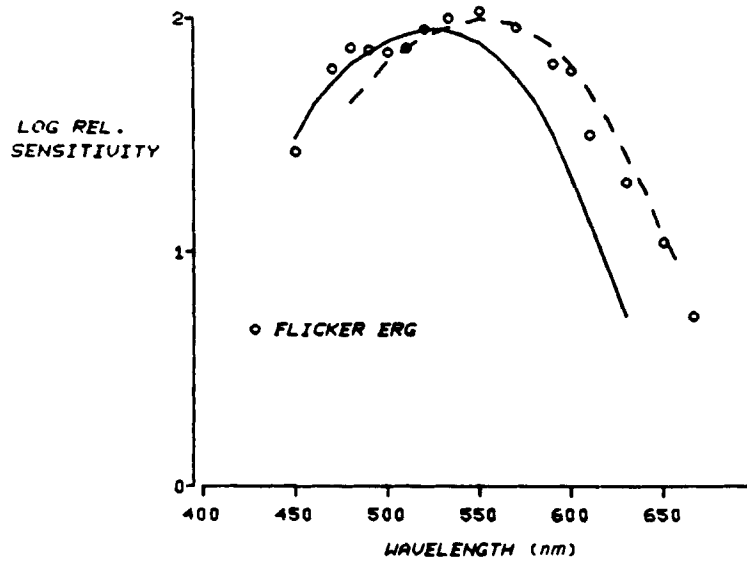


FIGURE 5. Log relative sensitivity as a function of wavelength for ERG flicker responses. The open circles are the means of three or four preparations (some wavelengths were used more frequently than others). The maximum SEM is 0.08 log units. The solid curve is an A_2 nomogram pigment with a λ_{max} of 520 nm. The dashed curve is an A_1 nomogram pigment with λ_{max} of 550 nm.

reciprocal of the energy necessary for a criterion response at each wavelength. Clearly, this is not the spectral sensitivity function of a single mechanism; there is a peak at 550 nm and a secondary hump at shorter wavelengths. Furthermore, the ERG flicker response waveform was quite different for different stimulus wavelengths, even when stimulus intensities were adjusted for approximately equal amplitude responses. For example, in Fig. 6 the response to 470-nm or 630-nm light are relatively simple with a single peak for each cycle of the stimulus, while the response to a 570-nm stimulus is frequency doubled—i.e. there are two peaks for each cycle of the stimulus.

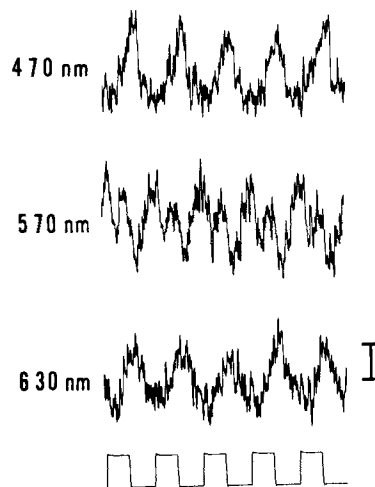


FIGURE 6. ERG responses to 10 Hz square-wave flicker. The numbers to the left of each record are stimulus wavelength. The calibration bar in the lower right represents 25 μV . The bottom trace represents the stimulus waveform. The trace duration is 0.5 s. The stimulus intensities in $\log \mu\text{W}/\text{cm}^2$ were -1.41 for the 470-nm light, -1.51 for the 570-nm light, and -0.89 for the 630-nm light.

The shift in the peak of the spectral sensitivity function indicates that the eel retina has some cones, like those found in many vertebrates, with a spectral peak at a wavelength longer than the peak wavelengths for the rods. The long wavelength part of the sensitivity function in Fig. 5 is approximately fit by an A_1 (Dartnall, 1962) nomogram pigment with a $\lambda_{\text{max}} = 550$ nm (dashed curve). However, the “flicker photometry” method was inadequate to isolate this long-wavelength mechanism from a short-wavelength mechanism. The short-wavelength mechanism might have been the rods which could not be suppressed fully by the background and 10-Hz flicker. Alternatively, another short-wavelength mechanism might have been involved. This is discussed below.

ISOLATED RETINA The bleached isolated retina preparation was used so as to remove completely all rod contributions to the ERG. This technique exploits the fact that cone pigment regenerates in the isolated retina after bleaching, but rod pigment does not (Zewi, 1939; Goldstein, 1967, 1970; Hood and Hock, 1973). After recovery from bleaching, the isolated eel retina gave ERG responses at different wavelengths like those shown in Fig. 7. It is clear

that response waveforms were not the same at different wavelengths. There was a dominant response at light offset (d-wave) for long wavelengths, and at light onset (b-wave) for short wavelengths. We obtained spectral sensitivity curves for the "on" response and the "off" response in these previously bleached isolated retinas; these curves are graphed in Figs. 8 and 9. We assert that these must be cone mechanisms because the rod pigment was irreversibly bleached away, and because there was no apparent peak in the sensitivity function near 520 nm.

Let us consider the long-wavelength cone mechanism first. In the *off*-response sensitivity function (Fig. 9) there is a peak roughly where the long wavelength mechanism in the flicker data peaked, at around 550 nm. The *on*-response sensitivity function (Fig. 8) has a shoulder in the long wavelength part of the spectrum. If the *on* and *off* functions are adjusted vertically, their long-wavelength portions are similar. The long-wavelength portion of the spectral

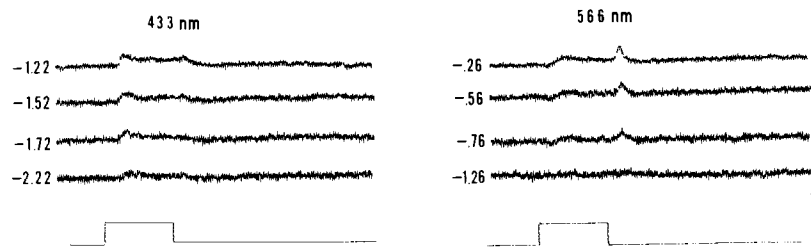


FIGURE 7. ERGs of the isolated eel retina which was bleached and then dark adapted. The left column shows responses to increasing intensities of 433-nm light. The right column shows responses to increasing intensities of 566-nm light. The numbers to the left of each record are the stimulus intensities in $\log \mu\text{W}/\text{cm}^2$. The calibration bar in the lower right represents 25 μV . The stimulus marker under each column is for a flash duration of 0.5 s.

sensitivity curves for the *on* response, *off* response, and flicker response are adequately fit by a vitamin A₁ pigment (Dartnall) nomogram, $\lambda_{\text{max}} = 550$ nm, the dashed curve drawn through each of these functions. We tried a number of pigment curves with different λ_{max} using both A₁ and A₂ nomograms (since this retina has both A₁ and A₂ pigments and it is not known which is in the cones). The 550 λ_{max} A₁ pigment curve gave the best fit to the data as a whole. However, the data are sufficiently noisy that strong conclusions about λ_{max} and A₁ vs. A₂ are not justified.

Now consider the really striking, and to us totally unexpected, peak in the blue-violet. This is a strong contributor to the ERG of the bleached, isolated retina. The peak is at a wavelength shorter than 450 nm. The short-wavelength mechanism produces an ERG response mainly at the onset of light. However, if the *on*- and *off*-response sensitivity functions (Figs. 8 and 9) are adjusted vertically, it can be seen that the short-wavelength portions are virtually identical. They are both fit by an A₂ nomogram pigment with a λ_{max} of 450 nm (solid curves). This short-wavelength mechanism might have contributed to the short-wavelength responses to the flickering stimuli used to isolate cones in the eyecup preparation, described above.

Rod-Cone Input to Horizontal Cells

The interneuron from which it was easiest to record in the eel retina was the horizontal cell which gives rise to the S potential. We only recorded L-type S

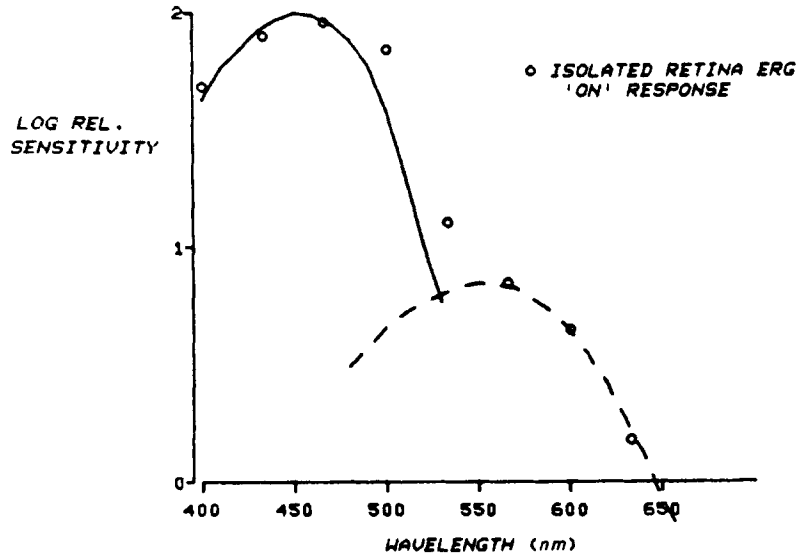


FIGURE 8. Log relative sensitivity as a function of wavelength for the ERG *on* response from the isolated retina. The open circles are the mean sensitivities for three preparations. The maximum SEM is 0.06 log units. The solid curve is an A₂ nomogram pigment for a λ_{\max} of 450 nm. The dashed curve is an A₁ nomogram pigment for a λ_{\max} of 550 nm.

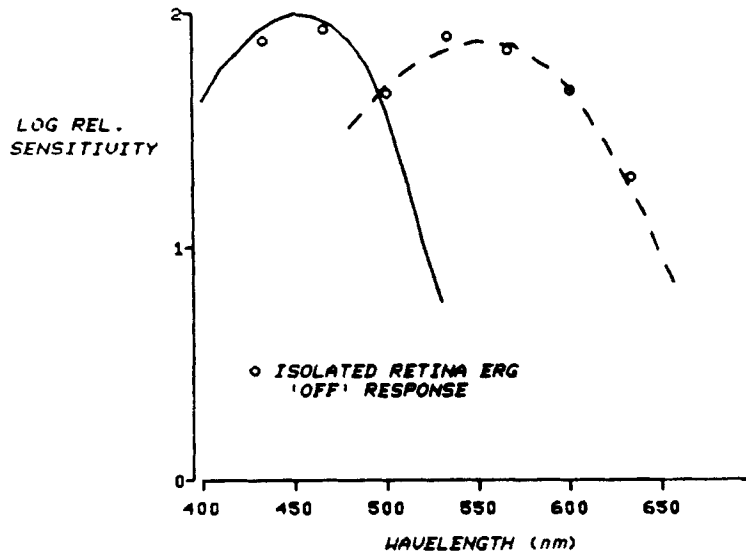


FIGURE 9. Log relative sensitivity as a function of wave-length for the ERG *off* response. Open circles represent mean sensitivities for three preparations. The maximum SEM is 0.09 log units. Pigment curves as in Fig. 8.

potentials in the eel. Since we know something about receptor classes in the eel retina, it was interesting to find out what we could about receptor-receptor interaction at the level of the S potential. This was done by measuring spectral sensitivities of S potentials, and also observing the response waveforms to stimuli of different wavelength.

Fig. 10 shows the spectral sensitivity of one out of several eel horizontal cells which gave very similar results. It can be seen that the sensitivity function is rod dominated at short wavelengths. The solid curve is for the rod visual pigment (A_2 nomogram, $\lambda_{\max} = 520$ nm). However, there is evidence for input to the horizontal cells from a long-wavelength cone mechanism, since at long wave-

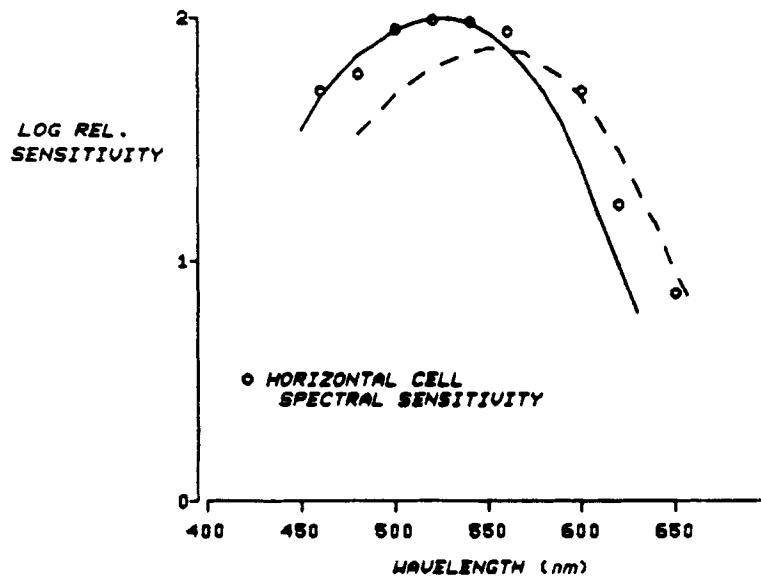


FIGURE 10. Log relative sensitivity as a function of wavelength for one eel horizontal cell. Open circles represent the mean of two measurements of sensitivity at each wavelength. The maximum SEM is 0.07 log units. Solid curve is an A_2 nomogram pigment for a λ_{\max} of 520 nm. Dashed curve is an A_1 nomogram pigment for a λ_{\max} of 550 nm.

lengths the measured sensitivity curve lies above the rod spectral sensitivity derived earlier (solid curve). In fact at long wavelengths, the spectral sensitivity of the horizontal cells may be accounted for by the 550-nm A_1 pigment curve which was used to fit the flicker and isolated retina ERG.

Further evidence for rod and cone inputs is found in the S-potential waveforms in response to high-intensity lights at different wavelengths, as illustrated in Fig. 11. The stimuli were flashed against a dark background and were chosen to give roughly equal responses. This means that about three times as intense a light was needed for the long wavelength stimulus, compared with the 460- and 480-nm lights. The saturated response of this horizontal cell was 20 mV. All three responses in Fig. 11 were about one-third the saturated amplitude, and their amplitudes lay on the linear portion of the response vs. log intensity curve. The responses at all wavelengths showed two time constants

of rise and two time constants of decay; the relative contribution of the "fast" and "slow" inputs varied with wavelength. Up to 460 nm, the response waveforms were driven predominantly by the slow input, presumably the rods. For the response at 480 nm, the fast decay was so much faster than the slow decay after light offset that there was a brief plateau in the off response. The change in the response waveform with wavelength, at a fixed response amplitude, is strong evidence for the input of at least two separate spectral mechanisms—probably the rods and the long wavelength cones. Similar arguments for rod-cone convergence onto horizontal cells have been used by others, e.g., Brown and Murakami (1968) for cat horizontal cells and Fain (1975) for mudpuppy horizontal cells. The changes in response waveform with wavelength are, if anything, more striking in the eel horizontal cells than in either cat or mudpuppy.

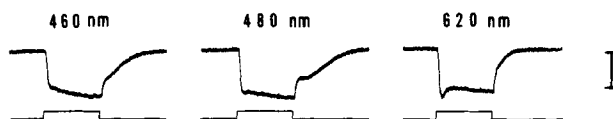


FIGURE 11. Eel horizontal cell responses. The numbers above each record are stimulus wavelength. The calibration bar represents 5 mV. The stimulus marker under each record represents a flash duration of 2.5 s. The stimulus intensities in $\log \mu\text{W}/\text{cm}^2$ were -3.13 for the 460-nm light, -3.26 for the 480-nm light, and -2.71 for the 620-nm light.

DISCUSSION

It is clear now that in the heavily rod-dominated eel retina there are at least two photoreceptor mechanisms in addition to the rods. At present we can make no definite statements about the identification of a particular photoreceptor mechanism with a particular receptor morphology. The spectral sensitivity of the short-wavelength mechanism is nearly the same as that of the "green" rods in amphibia (for references see Gordon and Hood, 1976), but also resembles the spectral sensitivity of "blue" cones found in other vertebrates (e.g., Marks, 1965), so it may be possible that the receptors which drive this mechanism are either rodlike or conelike in appearance. They might only physiologically be "cones," in the sense that they survive bleaching in the isolated retina, and are somewhat faster in response time than the 520-nm rods.

The fact that there are two conelike spectral mechanisms in the eel retina suggests that there might be the possibility of color vision in these animals. This prompted us to look for color-opponent retinal ganglion cells in the eel, of the type that are seen in monkeys which do have color vision (De Valois, 1965; De Valois et al., 1966; De Valois and De Valois, 1975). In preliminary experiments we observed evidence of color opponency. That is, responses of retinal ganglion cells to 480-nm diffuse light were *on-off* excitatory with sustained inhibition while the light was on, while responses to 600-nm light were excitatory to light onset, with sustained excitation while the light was on. This implies that the eel central nervous system is receiving signals from some of its retinal ganglion

cells which would enable it to perform color discriminations.

It is interesting that the rods and cones provide input to horizontal cells in the eel retina. One cannot say whether this is via direct synaptic connections from both receptor types onto horizontal cells or via rod-cone coupling and synaptic connection of horizontal cells to only one class of receptors. Nevertheless, it is one of the clearest examples, in fish, of receptor convergence onto a single horizontal cell (Orlov and Maksimova, 1965; Witkovsky, 1967; Naka and Rushton, 1968; Laufer and Millán, 1970; Kaneko and Yamada, 1972).

In all of the above respects, the eel retina may serve as a cold-blooded model for the human peripheral retina and the retinas of other mammals. In the accompanying paper we consider how neural signals from the distal part of the retina of the eel are summed to produce the responses of eel retinal ganglion cells.

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