A possible mechanism for color vision in the rat

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The ERG of the rat, evoked by equal energy flashes of monochromatic light in the dark-adapted eye, flashes superimposed on a bright "white" background, and flashes superimposed on chromatic backgrounds, was used to construct action spectra for the rat eye. These action spectra indicate that the rat retina contains more than one spectral mechanism. While these data are inadequate for determination of the number and spectral characteristics of the underlying mechanisms, the hypothesis that the rat has a single spectral mechanism mediated by rhodopsin must be rejected.

Color vision in mammals has classically been considered a property unique to primates. It seems highly unlikely, however, that a mechanism as complex as that which mediates the perception of color would not leave traces of evolutionary development in lower order mammals. Such traces would most likely be found at the simplest functional level, the retina, in the form of at least two pigments with different absorption spectra. One means of testing such a hypothesis is to determine the electroretinographic action spectrum from equal-energy flashes through the visible spectrum.

The species chosen for the present study is the rat. A wide variety of data suggest that this animal may have the necessary physiological mechanisms for rudimentary color vision. (See Massof & Jones, 1971, for a review of this problem.) The most direct evidence has been provided by behavioral studies demonstrating the rat's ability to make limited wavelength discriminations (e.g., Munn & Collins, 1936; Walton & Bornmeier, 1939). In addition, electrophysiological studies have provided indirect evidence of visual receptor activity characteristics of cones, a structure capable of mediating color vision (e.g., Granit, 1941; Dodt & Echte, 1961; Sokol, 1970; Massof & Jones, 1971). The purpose of the present study is to examine the rat electroretinogram (ERG) in order to determine the number and nature of the rat's visual pigments.

SUBJECTS

Six hooded rats and three albino rats were used in the present study.

APPARATUS

A 2-deg 100-msec monochromatic stimulus was provided by a Bausch and Lomb monochromator and presented in Maxwellian view. A 10-deg background was provided by a

tungsten source and was also presented in Maxwellian view. Wratten neutral density filters were used to control intensity and present an equal energy spectrum.

The evoked potential from the animal's eye was amplified (gain of 25,000) by an ac-coupled (0.01-Hz to 2.1-KHz bandpass) differential-input battery-powered amplifier with 1.5 microV internal noise. Fifty signals were averaged by a computer of average transients (CAT-1000) and plotted with an x-y ink writer.

PROCEDURE

The animals were anesthetized with 50 mg/kg of pentobarbital sodium and placed in a head holder. The left pupil

was dilated with cyclogyl and an AgAgCl ring electrode was placed on the cornea at the limbus. The reference electrode was placed on the cornea of its right eye. The prepared animals were then placed in an rf-shielded box and aligned with the optical system.

For all rats, the ERG was recorded for an equal-energy spectrum (420-640 nm in steps of 20 nm). Intense stimuli, well into the photopic range, were presented. For three hooded rats and two albino rats, the ERG to an equal-energy spectrum on a white adaptation background was recorded. The same procedure was repeated on one albino rat only using a red background and a blue background.

RESULTS

The mean b-wave amplitude of the ERG as a function of wavelength, for the no-background condition, is shown in Fig. 1. If rhodopsin were the only pigment present, it would be expected that the ERG would approximate the rhodopsin absorption spectrum. This is clearly not the case. Maximum b-wave amplitude occurs at 520 nm, and there is relatively high long-wavelength sensitivity. Also, the sharp change in the slope of the curve at short wavelengths suggests the intrusion of additional receptor mechanisms.

By using a white-light background, much of the rod response can be

Fig. 1. Mean B-wave amplitude of all rats is plotted as a percentage of the maximum response as a function of wavelength (solid line). This is compared with the rhodopsin absorption spectrum, plotted as percent of maximum absorption (dotted line).

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Fig. 2. Percent of maximum response amplitude of a representative hooded rat is plotted as a function of wavelength. Solid line is for the no-background condition and the dotted line is for the condition employing an adaptive white-light background.

eliminated from the total waveform. As can be seen from the data of a representative hooded rat (Fig. 2), white-light adaptation causes a relative enhancement of the 520-nm peak and reveals a 460-nm peak.

With chromatic adaptation it can be seen that the amplitude function shifts with a change in the color of the background (see Fig. 3). Again, if rhodopsin were the only pigment present, the shift would not occur. It is also interesting to note that a 580-nm maximum with blue adaptation is abolished when red adaptation is used.

The data of the present study suggest that in addition to rhodopsin, the rat possesses a short-wavelength pigment and at least one long-wavelength pigment. It can be postulated that the absorption maxima of these pigments are in the region of 460 to 480 nm and 520 to 580 nm. Whether the 520-nm peak is due to rhodopsin-generated activity interacting with the response generated by a longer wavelength pigment or if it is an absorption maximum of a single pigment cannot be determined at the present time.

DISCUSSION

Minor deviations of an action spectrum from a known absorption

spectrum are not uncommon. However, these deviations have certain characteristics. The most obvious case is the difference in the region of maximum absorption of rhodopsin in solution and the region of maximum sensitivity of the eye. This difference in the human is produced by absorption of short-wavelength light by the preretinal media and produces an action spectrum considerably narrower than the absorption spectrum of rhodopsin.

Measurement errors and changes in the preparation produce minor deviations in an action spectrum, but these deviations fall on both sides of the model with an overall good fit. While some of the data could be explained by postulating a strange absorption spectrum for the rat's preretinal media and some by experimental error, the chromatic adaptation data indicate a differential effect on more than one fundamental mechanism.

It might be argued that the short-wavelength peak is a result of rhodopsin bleach by-products. This suggestion, however, disagrees with the data of a more extensive study (Massof & Jones, 1972), which demonstrates that the x-wave of the ERG (a cone-generated potential) has

Fig. 3. Percent of maximum response amplitude of an albino rat is plotted as a function of wavelength. The condition using a blue adaptation background is represented with a solid line and the dotted line represents the red adaptation background.

maximum sensitivity in the same short-wavelength region of the spectrum. This, coupled with the present data, suggests a pigment different from rhodopsin.

The demonstration of more than one spectral mechanism in the rat retina indicates that the primary peripheral mechanism for color vision, pigments with different absorption spectra, exists. Whether the central mechanisms required to mediate the perception of color are present is yet to be determined.

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