Cone activity in the light-induced DC response of monkey retina

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In the rhesus monkey the action spectrums for eliciting DC responses and rod-mediated ERG’s are not identical. Long wavelengths are relatively more effective than short wavelengths in eliciting DC responses, indicating that cone receptors must be contributing to the DC response. The relative effectiveness of short wavelengths for evoking DC responses increases with dim light stimulation, suggesting that a Purkinje shift occurs.

Two action spectrums have been determined for the slow increase in the light-sensitive DC potential of the human eye. The similarity of both to the ICI scotopic luminosity function has led to the hypothesis that the DC response is mediated by the rod receptors alone. Some evidence is not easy to reconcile with this hypothesis. Human subjects without rod function can have large DC responses to light. The light energies which produce DC responses also activate cone vision. The action spectrum determined by Elenius and Lehtonen has a higher long wavelength sensitivity than the ICI scotopic function. Last, detecting the cone contributions to such a mass retinal response may be difficult because of the large ratio of rods to cones in the primate retina.

This study tests the hypothesis that the DC response of the retina following illumination is the result of rod-mediated activity alone by comparing the effectiveness of monochromatic lights for eliciting both rod ERG’s and DC responses in the rhesus monkey. If the DC response is produced by rods alone, the relative effectiveness of monochromatic lights for producing rod ERG’s and DC responses should be identical.

Methods

The methods are similar to those of the previous paper. Square-wave flicker with equal light-dark intervals at 4 c.p.s. was used to elicit ERG and DC responses simultaneously. The period of light stimulation was 800 seconds and was always preceded by 20 minutes of dark adaptation. The energy and wavelength of the light were changed by means of neutral and double interference filters, both calibrated spectrophotometrically. In order to minimize the effects of drift in the relatively long-term experiments, long and short wavelength stimuli were paired and each was used alternately at different light energies over a range of about 5 logarithmic units in each experiment; 456 ms was paired with both 583 and 610 ms and 442 ms with 610 ms. The amplitude of the DC response was measured from the DC level just prior to stimulation to the maximum amplitude of the response.

The spectral sensitivity of the ERG was found by determining the reciprocal of the relative light energies necessary to elicit approximately threshold responses with both 4 c.p.s. flicker and pulses of light at a number of different wavelengths. Light energies were measured with a glass-housed vacuum Thermopile and galvanometer. The ERG responses were obtained after 20 minutes of dark adaptation.
Results

Figs. 1 and 2 show ERG and DC responses obtained simultaneously with short and long wavelength stimuli at different intensities. With dim stimuli the short wavelengths produce larger ERG's than the long wavelengths and little or no DC responses are apparent. With brighter stimuli, long wavelengths produce proportionately larger ERG's as the cone system begins to make a contribution to the response. At this point prominent DC responses occur. The energies of the stimuli are changed in the same proportion for all wavelengths by means of neutral density filters. Therefore, the short wavelengths must always remain more effective for stimulating the rod system. The long wavelengths stimulus, 610 mµ, is slightly more effective than 442 mµ for producing DC responses, an effect that must be due to action of the cone receptors.

Fig. 3 shows the relationship between the amplitude of the DC response and the logarithm of the relative light energy energy in a number of such experiments with different long and short wave stimuli. The
Fig. 3. The relationship between normalized DC responses and the log relative energy of the stimulus at four different wavelengths. The wavelengths are shown as millimicrons in the small boxes.

Fig. 4. The spectral sensitivity for eliciting small ERG responses (25 to 50 μV) of constant amplitude after prolonged dark adaptation with either single pulses (0.24 second) (○) or 4 c.p.s. flicker (■). The hatched line connects the wavelengths which were paired in the study of the DC response. The continuous curve is the ICI scotopic luminosity function.

responses have been normalized to facilitate comparison; 610 mμ is seen to be relatively more effective than 442 mμ when the stimuli are bright.

Fig. 4 shows the action spectrum for eliciting threshold, dark-adapted ERG’s, a function which closely parallels the scotopic visibility curve for both man and the rhesus monkey. This function must also reflect the action spectrum of the rods in the rhesus monkey. The short wavelength stimuli used to elicit DC responses can be seen to be more effective for stimulating the rods than their long wave counterparts.

Fig. 5 shows the ratio of the responses obtained with pairs of short and long wave stimuli to the greater response of the pair. By comparing each response with another that occurred at a similar time, the effect of slow changes during the long-term experiments can be minimized. The ratios are plotted against the relative scotopic energy of the stimulus. Relative scotopic energies have been obtained from the action spectrum of the dark-adapted ERG (Fig. 4) by adding the logarithmic difference in ERG sensitivity between 442 mμ and the other wavelengths to the relative energy of each test wavelength. The cone contribution is most apparent when the DC responses to the stimuli from the extremes of the spectrum, 442 and 610 mμ, are compared. Except for the dimmest stimuli, 610 mμ is always more effective than 442 mμ in eliciting DC responses even though its scotopic
Cone activity in response of monkey retina

Fig. 5. The ratios of the amplitude of paired DC responses to the larger response of the pair plotted against relative scotopic energy. Each open circle has a corresponding closed circle immediately adjacent on the left except for the dimmest stimuli at 583 and 456 mµ where two responses at 456 were compared with one at 583 mµ.

effectiveness is always less. The relatively greater effectiveness of 442 mµ at dim light levels may be the result of a Purkinje shift.

Discussion

The fact that a long wavelength stimulus, shown to be less effective than a paired short wavelength stimulus for eliciting rod-mediated ERG’s, is more effective for eliciting DC responses indicates that the action spectrum for producing DC responses and scotopic ERG’s is not identical. The action spectrum for the scotopic ERG is shown to reflect rod activity. The action spectrum for the DC response must be more sensitive to long wavelengths, which undoubtedly reflects a cone contribution to the response. Physical factors, such as halation and lens absorption, which cause the action spectrums of retinal responses to differ from those that would be obtained at the receptor level, would affect both the scotopic ERG and the DC responses identically if they were mediated by the same receptor system.

REFERENCES