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Spectral sensitivity of ground squirrel cones measured with ERG flicker photometry

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Summary. Ground squirrels have dichromatic color vision. The spectral sensitivities of the two classes of cones found in the retinas of two species of ground squirrel were measured using ERG flicker photometry. The spectral sensitivity curves for these cone classes were closely fit by curves from wavelength-dependent visual pigment nomograms. One cone type had an average peak sensitivity of 518.9 nm (California ground squirrels, *Spermophilus beecheyi*) or 517.0 nm (thirteen-lined ground squirrels, *Spermophilus tridecemlineatus*). The second type of cone found in these ground squirrels had an average peak sensitivity of 436.7 nm. An examination of the variation in spectral sensitivity among individual animals suggests that the sensitivity peaks for the middle-wavelength cone cover a range of not greater than 4 nm.

Introduction

Ground squirrels are unusual among mammals in that they have cone-dominated retinas. In addition to a small population of rods (West and Dowling 1975; Jacobs et al. 1976; Long and Fisher 1983), probably comprising not more than 10% of all photoreceptors, there is both electrophysiological (Michael 1965; Gur and Purple 1978; Jacobs and Tootell 1981) and behavioral (Crescitelli and Pollack 1965; Jacobs 1978) evidence indicating the presence of two types of cones in these retinas. One of these has peak sensitivity in the short wavelengths, at perhaps about 440 nm (Jacobs and Tootell 1981). Both electrophysiological and behavioral results indicate that the other cone type is much more prevalent. There have been a number of specifications of the spectral location of peak sensitivity of this cone based on gross-potential and single-unit electrophysiology (Tansley et al. 1961; Crescitelli and Pollack 1966; Michael 1968; Jacobs and Yolton 1972; Green and Dowling 1975; Fisher et al. 1976; Jacobs et al. 1976; Tong 1977; Jacobs and Tootell 1981; Raisanen and Dawis 1983). These estimates cover a rather substantial range, from 516 to 535 nm, and it is natural to wonder if that range reflects species variations, differences in experimental approaches, or some inherent individual variations in the spectral positioning of cone photopigments.

We have recently developed an electroretinographic (ERG) technique for assessing spectral sensitivity based on the principle of flicker photometry that appears to offer a number of advantages over the more conventional means used to estimate spectral sensitivity from electrophysiological measurements (Neitz and Jacobs 1984). The approach is similar in concept to that recently also employed in a study of rabbit cones (Nuboer et al. 1983). We have used this technique on ground squirrels, and here report measurements of the spectral sensitivity of the cones in the two species of ground squirrels that have been the most frequent subjects for vision research.

Methods

Subjects. Adult, thirteen-lined (*Spermophilus tridecemlineatus*) and California (*Spermophilus beecheyi*) ground squirrels of both sexes were examined. The former were obtained from a supplier in Illinois, the latter were trapped locally. Prior to testing all were housed for several weeks under standard colony conditions.

Apparatus. Both the apparatus and general procedure are described in detail elsewhere (Neitz and Jacobs 1984). Briefly, stimuli were produced by a three-beam Maxwellian-view optical system. The test light originated from a Bausch and Lomb high-intensity grating monochromator having a tungsten-halide

source (half-energy passband = 10 nm). Its intensity was varied with a circular neutral density wedge (OD = 0.0–3.0). The reference light came from a tungsten-halide lamp. A third beam, used here for accessory adaptation, also originated from a tungsten-halide lamp. The characteristics of the latter two lights were controlled with neutral-density step filters and Ditric interference filters (half-energy passband = 10 nm). All lamps were underrun at 11 V from a regulated DC power supply. The outputs from these three beams were optically superimposed and presented to the eye in Maxwellian view (53°). Each channel of the optical system contained a high-speed electromagnetic shutter (Vincent Associates Uniblitz) driven from a programmable digital timer. Light measurements were made with a PIN 10 DF silicon photodiode (United Detector Technology).

ERGs were differentially recorded with a Burian-Allen bipolar contact lens electrode. The ground electrode was placed against the inside of the cheek. In the flicker-photometric procedure the ERG responses to a flickering monochromatic light are compared to the responses elicited by a similarly flickering, fixed reference light. The sequence of stimuli was: test light, no light, reference light, no light, etc., where all intervals were equal in duration. One such cycle is here referred to as stimulus frequency; note that flicker frequency is twice this value. The amplified ERG elicited by these stimuli was passed through an active, narrow bandpass filter, the center frequency of which was set to the stimulus frequency. The filter consisted of two two-pole stages (for each, Q = 5). The half-voltage bandpass of the filter was 0.2× center frequency. When the intensity of the test and reference light were greatly different, the output from this filter was roughly sinusoidal. A reversal of the relative intensities of the two lights produced a phase reversal of the sinusoidal output from the filter. At intermediate intensities of the two lights, the amplitude of the resultant signal was minimized and its phase intermediate. To improve the cancellation achieved at this point, the output from the filter was passed through a second narrow bandpass filter. In this case the center frequency of the filter was set to the flicker frequency. That output was in turn averaged with an Ortec Model 4623 Signal Averager such that the signal produced by the reference light was averaged with the inverted signal from the test light (Neitz and Jacobs 1984). The signal averager output was displayed on an oscilloscope.

Procedure. Ground squirrels were anesthetized with IP injections of sodium pentobarbital (75 mg/kg). The pupil of the test eye was dilated (Phenylephrine HCl + 0.04% atropine sulfate). The animal was placed in a stereotaxic instrument and aligned with the test beam. Normal body temperature was maintained through the use of a circulating hot water heater.

As noted, spectral sensitivity was measured with a flicker photometric procedure. The following conditions were used to measure spectral sensitivity of the ground squirrel middle-wavelength cone. The flicker rate was 50 Hz. The reference light was achromatic and had a corneal radiance of 33 μW. The test light was taken from the monochromator as described above. The measurements were made in the presence of a short-wavelength adaptation light (wavelength = 440 nm; corneal radiance = 115 μW). The purpose of this chromatic adaptation was to further eliminate the possibility of any contribution from the short-wavelength cones to the 50 Hz flicker. All the recording was done in a lighted room. As measured at the cornea these overhead lights yielded a luminance of 60 cd · m^{-2}.

To measure the spectral sensitivity of the ground squirrel short-wavelength cone, the flicker rate was set to 25 Hz. A monochromatic short-wavelength light (440 nm, corneal radiance = 71 μW) was used as the reference. The test light was again drawn from the monochromator. To provide a long-wave-length adaptation light, a high pass filter was placed in the adaptation beam (Kodak no. 23 A; 50% transmittance = 590 nm). Several adaptation intensities were employed in different experiments (corneal radiance from 283 to 639 μW).

To make a sensitivity measurement, the density wedge was first set to an arbitrary position. A train of 100 stimulus cycles was presented and the responses to the last 60 of these were averaged. The phase and amplitude of that response was used to indicate the change in wedge setting required to better null the response to the reference light. This procedure was done iteratively until the best null position was found. Sensitivity measurements were usually made at successive 10 nm steps with frequent rechecking throughout the course of the experiment.

To determine spectral sensitivity, the final wedge settings at each test wavelength were corrected for the spectral transmittance of the wedge, for the variations in the monochromator output at different wavelengths and for lens absorbance in these species (Yolton et al. 1974). These corrected values were compared to wavelength-dependent visual pigment nomograms using the polynomial expressions provided by Dawis (1981). A computer was used to determine the spectral position (to the nearest nm) of that nomogram which gave the best fit to the spectral sensitivity values. To do this the difference squared between each sensitivity value and the nomogram was computed for each of the possible nomograms. The nomogram providing the smallest average difference squared was selected as best fitting the data.

In determining the spectral sensitivity of the short wavelength mechanism it proved impossible to completely isolate the responses from a single cone class, and so in those experiments two other nomogram fitting procedures were employed. Both were based on the assumption that the flicker spectral sensitivity functions reflect linear summation of two spectral mechanisms, each having the sensitivity of a nomogram photopigment. In one procedure the λ_{max} value for one of the two mechanisms was specified by the operator and the computer determined the λ_{max} value of the other nomogram mechanism needed to yield the best summed fit of the two. In the other variation the computer was employed to determine the λ_{max} values of the two spectral mechanisms required (when summed) to best fit the observed spectral sensitivity function. In both cases, the computer determined the spectral location(s) of peak sensitivity to the nearest nm and the relative proportions of the two components, as well as the goodness of fit for the best fitting combination.

Results

In earlier measurements made on monkeys we showed that the flicker photometric procedure provides a very sensitive and reliable tool for assessing spectral sensitivity (Neitz and Jacobs 1984). The technique proved to be at least as sensitive with ground squirrels as with monkeys; as in that earlier experiment, changes in the wedge setting from the null position on the order of 0.02 to 0.04 log unit usually produced clearly discriminable changes in the ERG output.

Middle wavelength cones

Figure 1 shows spectral sensitivity functions obtained from six 13-lined ground squirrels recorded

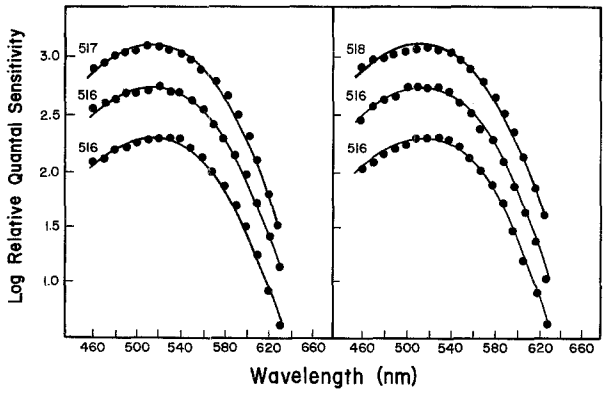

Fig. 1. Flicker photometric spectral sensitivity functions for six thirteen-lined ground squirrels obtained under conditions (see text) which isolate the activity of the middle wavelength cone in this species. Solid circles are sensitivity values obtained by equating the effectiveness of monochromatic test lights and an achromatic reference light. These values have been corrected for absorbance by the lens. Solid lines are the best fitting visual pigment nomogram, the spectral peak of which is indicated on each function. Curves are arbitrarily positioned on the sensitivity axis

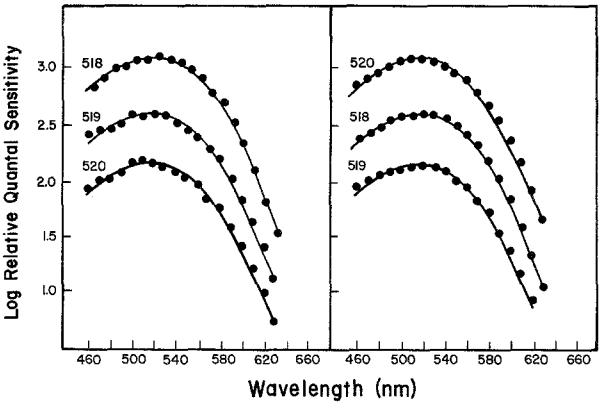

Fig. 2. Flicker photometric spectral sensitivity functions for six California ground squirrels. All other details are the same as given in Fig. 1.

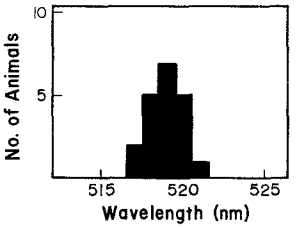

Fig. 3. Frequency distribution showing the spectral peaks of the middle-wavelength cone for twenty California ground squirrels. Each peak was derived from a curve of the type illustrated in Fig. 2. For this distribution the mean spectral peak is 518.9 nm (SD = 1.07). Bin width, 1 nm

under conditions which appear to isolate the activity of the middle wavelength cones. The solid circles are sensitivity values corrected as described above; the solid lines are the sensitivity curves for the best fitting visual pigment nomogram. The λ_{max} value determined for each animal is indicated on the individual curve. All peaked at either 516, 517 or 518 nm. It can be seen that without exception these nomograms provide very good fits to the sensitivity data. The fitting errors generated from this procedure were small (mean squared difference $= 2.8 \times 10^{-3}$ log unit). Figure 2 shows similar results obtained from six California ground squirrels, all of whom were run under the same conditions. In this case the peak locations were 518 to 520 nm. These data are also well accounted for by the nomogram curves (mean squared difference $= 1.8 \times 10^{-3}$ log unit).

Individual variability

A noteworthy feature of the results presented in Figs. 1 and 2 is the small individual variation in the location of the spectral peak of the best fitting nomogram. That variation was only 3 nm for the 13-lined ground squirrels and for the California ground squirrels. Those results are based on relatively small samples. To gain a clearer indication of the magnitude of individual variation in this measure in the population we ran additional California ground squirrels under the same test conditions. In each case a best fitting nomogram was derived. The results of this experiment for a total of 20 ground squirrels are summarized in the form of a frequency histogram in Fig. 3. These results verify that there are only small individual variations in the spectral positioning of the middle wavelength cone in the ground squirrel. For the 20 animals the mean λ_{max} value was 518.9 nm (SD = 1.07). Both of these descriptors are close to those characterizing the more limited sample shown in Fig. 2.

Figure 3 provides an indication of the variation in the spectral sensitivities of the middle wavelength mechanism in the ground squirrel as measured with ERG flicker photometry. It is of interest to ask what might underlie this variation. One can imagine at least two separable sources accounting for this variation: (1) inherent individual variations in the eye (reflecting, for example, variations in the spectral absorbance of the photopigment or individual variation in preretinal filtering), or (2) inherent variations introduced by the measurement procedure. To see if these potential sources of variation could be better separated, a second experiment was performed. For this a male California

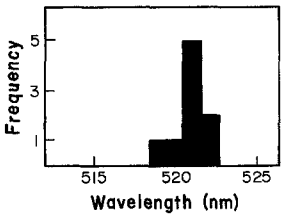

Fig. 4. Frequency distribution showing the spectral peak of the middle wavelength cone derived from repeated testing of a single California ground squirrel. The mean spectral peak is 520.9 nm (SD = 0.93). Bin width 1 nm

ground squirrel was repeatedly tested over a period of several months until a total of nine complete spectral sensitivity functions had been determined. The procedure used for each such determination was identical to that used in the experiments just described. The animal selected as a subject for this experiment was one who on initial examination had a spectral sensitivity function representing a clear deviation from the sample mean of Fig. 3 – the best fitting nomogram for this animal on this initial test had a peak at 521 nm. The results of this experiment are summarized in Fig. 4.

This distribution had a mean value of 520.9 nm with an SD = 0.93. Although the absolute difference in the estimate of the peak of the spectral sensitivity function for this animal obtained from repeated tests from that of the larger sample is small, it is statistically very reliably different (one sample t-test, $t = 6.79$, $df = 8$, $P < 0.001$). Thus it may be concluded that reliable individual variations in spectral sensitivity can be found in the ground squirrel.

Given that there are real differences in spectral sensitivity among ground squirrels, is it possible to further partition that variability? If the individual variations were due to some fixed feature of the eye, it would be expected that the variability in the peak measured for the individual animal should be smaller than the variability in the same measure across animals. To examine this we compared the variance measure for the sample of Fig. 3 and the variance determined for the repeated measures on the individual ground squirrel. The ratio of these two variances is 1.33. An F test was used to obtain the confidence interval for the ratio of these two measures in the population. Those limits were 0.32 and 2.58 ($df = 19,8$; $P < 0.05$), and thus the hypothesis that these two variances are the same cannot be rejected. To the extent that the variance from the measurements on the individual animal represent error in the measurement procedure, and the variance from the measurements on the twenty animals reflect measurement error plus

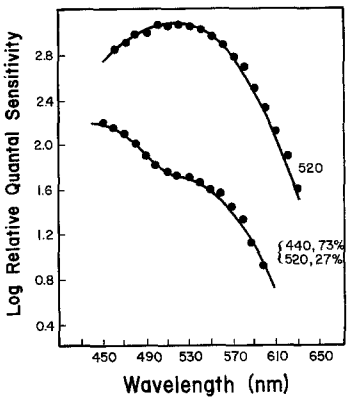

Fig. 5. Flicker photometric spectral sensitivity functions obtained from a California ground squirrel. The function at the top was obtained under conditions which isolate the activity of the middle wavelength cone (see text). The continuous line is the curve for the best fitting visual pigment nomogram, the spectral peak of which is indicated. The bottom function shows a redetermination of spectral sensitivity recorded under conditions which favor a contribution from the short-wavelength cone (see text). The continuous line used to fit the bottom function represents the summation of the two nomogram pigment curves which gave the best fit to the experimental data. The peaks of these curves and their relative proportions are indicated. The vertical positioning of the two functions accurately reflects the threshold elevation produced by the adaptation condition used to obtain the data shown at the bottom

inherent individual variability, it may be concluded that at least 0.32 of the variability in the spectral peak location among the latter animals can be attributed to measurement error. Since the total range of spectral peak locations for the middle wavelength cone is not apt to exceed 6 nm (ca. 6 SDs), this analysis implies that the actual variation in spectral peak location is not greater than 4 nm.

Short wavelength cones

In earlier experiments we found that a signal from the ground squirrel short-wavelength cones could be readily detected in ERGs recorded in the presence of intense long-wavelength adaptation (Jacobs and Neitz 1984). In this investigation we used ERG flicker photometry to try to determine more precisely the spectral sensitivity of this mechanism. The subjects were California ground squirrels.

A variety of chromatic adaptation and flicker rate combinations were first explored to find those conditions which maximized the contribution to the ERG from the short-wavelength mechanism. Fig. 5 shows results from an experiment which achieves this goal.

At the top of Fig. 5 is a spectral sensitivity function recorded under conditions thought to

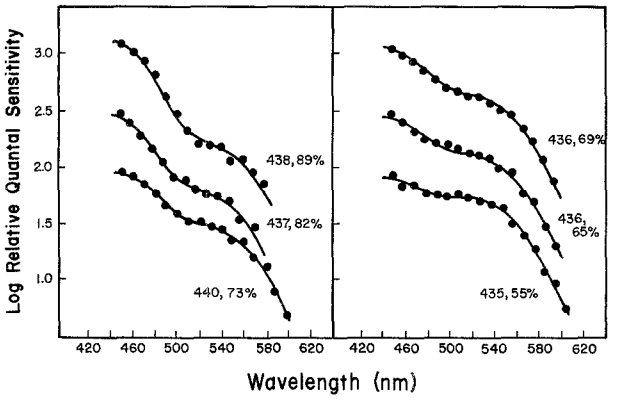

Fig. 6. Flicker photometric spectral sensitivity functions obtained from California ground squirrels under conditions favoring contribution from the short-wavelength mechanism. In each of the six cases the continuous curve is that for the best fitting linear summation of two nomogram pigment curves. In each, one of the components had a peak set at 519 nm. The wavelength and relative proportion of the short-wavelength component required to complete the best fit are indicated on each function. Note that although the degree of isolation of the short-wavelength component varied substantially in these experiments, the derived peak of the short-wavelength mechanism varies nonsystematically over a small spectral range. The curves are arbitrarily positioned on the sensitivity axis

isolate the middle wavelength cone. As before, the data are well fitted by a nomogram having a peak at 520 nm. The lower curve was obtained from the same animal using 25 Hz flicker, a 440 nm reference light, and concurrent long-wavelength adaptation. This adaptation produced a large decrease in sensitivity (ca. 1.3 log units at 520 nm) and yielded a sensitivity function in which the contribution from the short-wavelength mechanism predominates. The curve drawn through the data points is the best fitting linear summation of two nomogram curves. To derive this curve, all pairwise combinations of nomograms having λ_{max} drawn from the ranges of 435 to 445 nm and 514 to 521 nm respectively were examined. The best fitting function so determined had the following components: 440 nm (73%) + 520 nm (27%). The fit of this combination to the data is excellent (mean squared difference = 2.30×10^{-4} log unit).

Additional animals were tested under conditions similar to those just described. In each of seven such experiments the derived peak for the middle wavelength mechanism was close to that found in the earlier experiments (mean = 519.8 nm, SD = 0.7). Consequently, in later experiments the curve fitting was simplified by specifying the peak of one component at 519 nm and then searching for the second nomogram which provided, in combination, the best fit to the data points. The results are shown for six ground squirrels in Fig. 6. Note that although the effectiveness of the isolation of the short wavelength cone varied from experiment to experiment, the peak of that mechanism was always located over a short spectral range, from 435 nm to 440 nm. For a total of twenty-one such determinations, the proportion of the short wavelength component required in the best fitting function was not correlated with the position of its spectral peak ($r = 0.10$, $df = 19$, n.s.). Most ground squirrels were tested under several conditions. For ten animals the best estimate of the spectral peak of the short wavelength component varied from 433 to 440 nm, with a mean value of 436.7 nm (SD = 2.6).

Discussion

The flicker photometric procedure yields a clear and consistent picture of the spectral properties of the middle wavelength cones in the ground squirrel. The average peak location for the California ground squirrel is 518.9 nm (N = 20); for the thirteen-lined ground squirrel it is 517.0 nm (N = 7). In both cases the shapes of the spectral sensitivity functions are well accounted for by curves derived from wavelength-dependent visual pigment nomograms.

With one exception (Raisanen and Dawis 1983), all of the previous studies of the ground squirrel, including those done earlier in this laboratory, yielded peak estimates of the middle wavelength cone that were at somewhat longer wavelengths than those presently found. We believe the current study gives a more accurate indication of the spectral location of this cone type than those done earlier for three reasons: (1) the number of spectral points examined and the number of individuals tested were considerably larger in this study, (2) none of the earlier studies employed automated curve fitting procedures (in our experience it is difficult to fit spectral sensitivity data by eye with standard curves to an accuracy of better than about 5 nm), and, perhaps most important, (3) the flicker photometric procedure is more sensitive and reliable than the single flash procedures typically used in the past. Our results are in good agreement with those of Raisanen and Dawis (1983) who, although using different ERG measures, also employed nomogram fitting techniques like those used in this experiment. For the photopic b-wave of the thirteen-lined ground squirrel their experiments yielded a spectral peak of 516 nm, while examination of the isolated PIII component of the ERG produced a peak estimate of 518 nm.

The spectral sensitivities of the middle wave-

length cones of California and thirteen-lined ground squirrels are very similar. This finding is in accord with results from behavioral studies in which no significant differences were detected between the two species in either color vision or visual sensitivity (Jacobs and Yolton 1971).

Measurements of the spectral peak of the ground squirrel short-wavelength cone were of necessity made less directly. Two assumptions on which the adequacy of that specification depends should be noted. The first assumption is that only two spectral mechanism contribute to the flicker sensitivity curve. As noted above, in addition to the two cone types, ground squirrel retinas contain a small population of rods, and a spectral mechanism with a 500 nm peak can be detected in the ERG recorded under certain conditions. Although we cannot rigorously exclude the possibility that the 500 nm mechanism is operative under the conditions used to measure the short-wavelength cone, it appears very unlikely to have had any significant effect. In addition to the fact that the stimulus conditions would be unfavorable for obtaining a signal from that mechanism[1], the stronger argument against their participation is that the peak of the middle wavelength cone derived from 25 Hz flicker was the same as that measured at much higher flicker rates. If the 500 nm mechanism were a contributing factor at the lower flicker rates one would expect the derived long-wavelength peak to have been shifted from 519 nm toward the shorter wavelengths. As noted, no such shift occurred (see Fig. 5). A second assumption is that the signals from the two cones are linearly summed to produce the flicker sensitivity curve. That same assumption has often been made in other flicker measurements of spectral sensitivity (cf. King-Smith and Carden 1976). Three results from this experiment support this assumption: (a) the fact that linear summation of the two nomograms always provide excellent fits to the spectral sensitivity curves, (b) the fact that the range of derived peak locations is small, and (c) the fact that the spectral peaks of the cone mechanisms derived with this procedure are unrelated to the relative proportions of the two components required to best fit the spectral sensitivity curve.

In previous electrophysiological experiments on ground squirrels there has been (apparently) only one attempt to specify the spectral properties of the short wavelength cone. In that experiment the spectral sensitivities of spectrally-opponent optic nerve fibers in the California ground squirrel were measured (Jacobs and Tootell 1981). We have now reanalyzed those data using the curve fitting procedures of the present investigation. For ten spectrally-opponent optic nerve fibers tested in the presence of intense long-wavelength adaptation, the spectral sensitivity of short wavelength mechanism had an average peak location of 441 nm. A behavioral experiment on golden-mantled ground squirrels yielded a peak estimate for the short-wavelength mechanism at 440 nm (Jacobs 1978). The conclusion from these studies as well as from the current experiment is that the short-wavelength cone of the ground squirrel has a peak close to 440 nm.

We return, finally, to the issue of individual variation in cone spectral sensitivity. In this investigation it proved possible to establish the degree of such variation in a large sample of subjects, and by making repeated determinations on an individual animal estimate how much of that variation might be attributed to measurement error, how much might reflect intrinsic differences between animals. The conclusion was that the actual range of variability in the spectral peak location of the middle wavelength cone in the ground squirrel is not apt to exceed 4 nm. This result may seem surprising if one views it with the suspicion that gross potential measures like the ERG cannot provide very precise indications of visual system physiology. However, this experiment, like previous ones (Nuboer et al. 1983; Neitz and Jacobs 1984), shows this suspicion is unfounded, that ERG flicker photometry can indeed provide a very reliable and sensitive tool for measuring spectral sensitivity.

The question of individual variations in cone spectral sensitivity has been discussed in conjunction with measurements made on humans. Both psychophysical (Alpern and Pugh 1977; Alpern 1981) and microspectrophotometric (Dartnall et al. 1983) results suggest that there may be significant individual variations in the spectral sensitivity of what have classically been considered single cone types. For instance, measurements made on human dichromats indicate that the spectral peak

1 Rods constitute a small minority (5–10%) of the photoreceptors in the ground squirrel retina, and their contributions have often been difficult to see even under optimal conditions. Even so, three separate features of the stimulus conditions used in this experiment would be expected to further militate against rod contributions: (1) Previous results from both behavioral (Jacobs 1978) and ERG (Jacobs and Tootell 1977) experiments indicate that the ambient illuminance in the recording room is well above that required to produce a Purkinje shift in the ground squirrel; (2) The adapting light yielded a retinal illuminance of 7.45×10^{-5} scotopic lumen $\cdot$ mm^{-2}; this value is more than 0.6 log unit higher than that required to saturate human rods (Aguilar and Stiles 1954); (3) The flicker rate (25 Hz) is probably well up toward the upper limit of the rod operating range

of the long wavelength cone may vary among individuals over a range of 8 to 11 nm (Alpern and Pugh 1977; Alpern 1981). To the extent that the present measurements and the human measurements are comparable, it appears that there is a source of individual variability in the human not seen in the ground squirrel. One distinct possibility already suggested (Alpern 1981; Dartnall et al. 1983), and perhaps made even more plausible by the ground squirrel measurements, is that what has been believed to represent a single spectral mechanism in the human actually reflects the presence of cones with more than one absorption spectrum. Whether that is true remains for future research, but it is at any rate clear that the range of spectral variability currently claimed for human cones is not a characteristic of all mammalian cones.

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