

## SPECTRAL MECHANISMS AND COLOR VISION IN THE TREE SHREW (*TUPAIA BELANGERI*)

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(Received 2 August 1985; in revised form 8 October 1985)

**Abstract**—The retina of the tree shrew (*Tupaia belangeri*) is heavily cone dominated, rods comprising less than 4% of the total photoreceptors. Spectral mechanisms and color vision were investigated in this species in both behavioral and electrophysiological experiments. In confirmation of an earlier investigation, the tree shrew was found to have a clear spectral neutral point (at ca 505 nm) and is thus a dichromat. Spectral sensitivity functions determined in an increment threshold discrimination task show two clear peaks (at ca 440 and 550–560 nm) with an intermediate region of lowered sensitivity centered at about 500 nm. Spectral sensitivity of the two cone types in this animal were determined using ERG flicker photometry. One of these cone classes has a peak at 556 nm; the other has a 444 nm peak.

Tree shrew *Tupaia belangeri* Spectral mechanisms Dichromacy

### INTRODUCTION

The anatomy and physiology of the tree shrew visual system have attracted much study. This is partially a consequence of the heated debate over the taxonomic status of these animals, that is whether they are primates, insectivores, or deserve unique classification (Luckett, 1980), and partially because the visual systems of these animals possess some of what are often considered to be extreme adaptations to diurnal life. Among mammals only the ground-dwelling sciurids appear to have a similar set of diurnal visual characteristics, and like those animals tree shrews were once thought to have pure cone retinas (Walls, 1942). As in the case of those sciurids (West and Dowling, 1975; Jacobs *et al.*, 1976) it is now known that the *Tupaia* retina also contains a small population of rods (Bunt and Klock, 1980; Immel, 1981; Kuhne, 1983). According to Immel (1981), rods comprise 3–4% of the total receptor complement in *T. belangeri*.

In contrast to the attention paid to the anatomy and physiology of the tree shrew visual system, there has been relatively little study of their visual behavior. Two visual capacities have been investigated. One of these, spatial acuity, has been recently re-examined (Petry *et al.*, 1984). The other is color vision. After investigations which showed that tree shrews could make some color discriminations (Tigges, 1963; Shriver and Noback, 1967), Polson (1968)

conducted a thorough examination of color vision in *T. glis*. She found the tree shrew to have clearly defined dichromatic color vision, similar in character to that of human deutanopia. The spectral mechanisms underlying this capacity remain unspecified. The electroretinogram (ERG) recorded from *T. glis* was found to have an average peak sensitivity of 552 nm with estimates from individual animals ranging from 540 to 570 nm (Tigges *et al.*, 1967). These same spectral sensitivity functions show a secondary peak in the short wavelengths, the location of which is poorly defined. The intent of the present investigation was to seek a specification of the spectral mechanisms in the tree shrew. To accomplish this we made both behavioral and electrophysiological measurements on *T. belangeri*.

### METHODS

#### Subjects

The tree shrews (*T. belangeri*) were colony reared. All were adults at the time of examination.

#### Behavioral experiments

The apparatus and general procedures for making behavioral measurements of color vision and visual sensitivity in nonhuman subjects have been described in detail (Jacobs, 1983, 1984). Briefly, a three-alternative, forced-choice discrimination task is used. The animal is

trained to select a uniquely illuminated stimulus panel from among three such panels. The two negative panels are illuminated identically to one another. The three panels (2.5 cm dia) are mounted in a row along one wall of a test chamber. A correct discrimination, indicated by a touch on the uniquely illuminated panel, is reinforced by delivery of 0.1 ml of grape juice. Over trials the panel receiving unique illumination is alternated randomly among the three. An optical system located outside of the test chamber permits the experimenter to control and vary the difference in the illumination of the positive and negative panels, and by so doing establish the threshold differences required for discrimination. All of the functions of the test apparatus are computer controlled.

(1) *Neutral point test.* We first sought to verify Polson's (1968) conclusion that this species has dichromatic color vision by searching for a spectral neutral point. The light illuminating the positive panel for this test was monochromatic; it was produced by an Instruments SA, Model H-10 grating monochromator (half-energy passband = 16 nm). The light illuminating the negative panels was achromatic (4800 K) held at a constant luminance of  $3.5 \text{ cd/m}^{-2}$ . Over trials animals were required to discriminate the monochromatic from the achromatic lights as the wavelength of the former was varied from 475 to 514 nm in steps of 3 nm. The intensity of the monochromatic light was varied in steps of 0.1 log unit over a range of  $\pm 0.6$  log unit around the intensity values required for a normal human trichromat to set the monochromatic and achromatic lights to equal brightness. Test trials were 2 sec in duration with a 4 sec intertrial interval.

Two male tree shrews were first trained to discriminate lights of 514 and 475 nm from the achromatic light. The intensity of these lights was changed every 5 trials to cover the range noted above. The tree shrews completed 200–250 trials in each daily session. Once the animals were consistently discriminating the 475 and 514 nm lights at all of the intensity values, the test was expanded to include all of the intermediate wavelengths. Each wavelength/intensity combination was presented for 5 trials and then changed to a new value. The process continued over test sessions until a total of 25 trials had been accumulated at each wavelength/intensity combination.

(2) *Increment-threshold spectral sensitivity.* An increment threshold procedure was used to

measure spectral sensitivity. The three stimulus panels were continuously and equally illuminated with achromatic light (4800 K). A test trial consisted of adding light from the monochromator to one of the three panels. As before the location of the positive panel was changed randomly over trials. Sensitivity was measured for test wavelengths from 440 to 660 nm in steps of 10 nm. At each test wavelength the intensity of the light was varied in steps of 0.3 log unit over a range sufficient to bracket performance from a level of greater than 90% correct down to chance. Depending on the wavelength, this required from 4 to 6 intensity steps. As in the previous test, wavelengths were tested in random order in each session with individual intensity/wavelength combinations in blocks of 5 trials.

After initial familiarization with the task the two tree shrews were further run over the entire span of wavelength/intensity combinations until their performance was asymptotic. At that point an additional 25 trials were run at each of the combination values. From these results psychometric functions were drawn for each test wavelength and threshold was defined as the panel irradiance required to maintain performance at an average level of 57% correct (95% confidence level). Complete spectral sensitivity functions were determined on two different achromatic backgrounds (luminances of 5 and  $25 \text{ cd/m}^{-2}$ ).

#### *Electrophysiological experiments*

Spectral mechanisms in the tree shrew retina were examined using ERG flicker photometry. Details of the optical system employed and of the flicker photometric procedure are given elsewhere (Neitz and Jacobs, 1984); hence only a brief summary of these features will be presented here.

Stimuli were produced by a three beam optical system. One beam (the test light) came from a monochromator (half-energy = 10 nm). A second beam (the reference light) and a third beam (used for accessory adaptation) both originated from tungsten halide lamps. Each beam could be independently shuttered and all were optically superimposed so as to form a Maxwellian view (53 deg).

ERGs were differentially recorded with a bipolar contact lens electrode. A ground electrode was placed against the inside of the animal's cheek. Flickering stimuli from the test and reference lights were interleaved. The individual

flashes were equal in duration and there was a dark interval equal in duration to the test and reference lights interposed between successive flashes. The ERG elicited by these lights was passed through active, narrow bandpass filters (bandpass =  $0.2 \times$  the center frequency). When the effectiveness of the test and reference light was greatly different, the filtered output was roughly sinusoidal. A reversal of the relative intensities yielded a phase reversal in the ERG. At intermediate intensity ratios the amplitude of the ERG was minimized and the phase intermediate. The ERGs were averaged (Ortec Model 4623) and displayed on an oscilloscope.

Tree shrews were anesthetized with an IM injection of 8 mg Ketamine hydrochloride plus 0.08 mg acepromazine maleate, and by subsequent IP injections of  $10 \text{ mg} \cdot \text{kg}^{-1}$  of sodium pentobarbital. Atropine sulfate was used to limit mucus secretions. The pupil of the test eye was dilated by topical application of atropine sulfate (0.04%) and Phenylephredine HCl. The animals were placed in a stereotaxic instrument. Normal body temperature was maintained through the use of a circulating hot water heater.

To establish a photometric equation a density wedge in the test beam was set to an arbitrary position. A train of 100 stimulus cycles (each cycle consisting of test light + reference light + intervening dark intervals) was presented and the response to the last 60 of these was averaged. The phase and amplitude of the response was used to determine the change in the intensity of the test beam required to better null the response to the reference light. The procedure was repeated until the best null position was determined and that density value was recorded. Spectral sensitivity measurements were made at 10 nm intervals.

Spectral sensitivity functions were determined for two conditions. In the first the long wavelength cone of the tree shrew was studied. Flicker rate was set to 62.5 Hz. The reference light was achromatic (corneal radiance = 0.05 mW). An accessory short wavelength adaptation light of 440 nm (corneal radiance = 0.15 mW) was continuously present. The purpose of this light was to further assure that the ERG would contain no contributions from the short wavelength cone. All of the recording was done in a lighted room (luminance measured at the cornea =  $60 \text{ cd/m}^{-2}$ ). A second set of flicker photometric measurements was made to specify the short wavelength cone.

For these the flicker rate was 25 Hz, the reference light was 460 nm (corneal radiance = 0.05 mW), and a long wavelength adaptation light was used to depress the sensitivity of the middle wavelength cone. The latter was produced by inserting a high pass filter (50% transmission = 592 nm; corneal radiance = 3.85 mW) in the adaptation beam.

To derive spectral sensitivity functions the final wedge settings at each test wavelength were corrected for the spectral transmittance of the wedge, for spectral variations in the monochromator output, and for absorption by the tree shrew lens (Tigges *et al.*, 1967). A computer was used to determine the spectral positioning (to nearest nm) of the visual pigment nomogram which best fit the data (Neitz and Jacobs, 1984).

## RESULTS

### Neutral point

Both subjects learned to successfully discriminate 475 and 514 nm lights from the achromatic light over the full span of intensity values. When the test wavelength was varied over the intermediate range, discrimination performance deteriorated. Figure 1 summarizes the performance levels achieved by each subject.

The data points are mean values for the final 25 test trials at each test wavelength. Plotted are the lowest levels of performance achieved at each test wavelength, values which are pre-

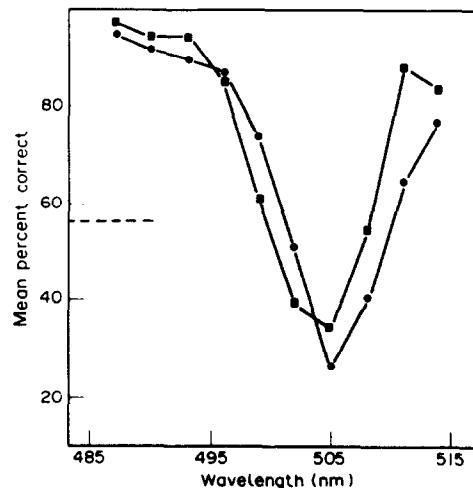


Fig. 1. Neutral point test results for two tree shrews. Each plotted point represents the performance achieved in a discrimination between achromatic and equiluminant monochromatic lights. The horizontal dashed line (right) indicates the performance required at the 95% level of confidence.

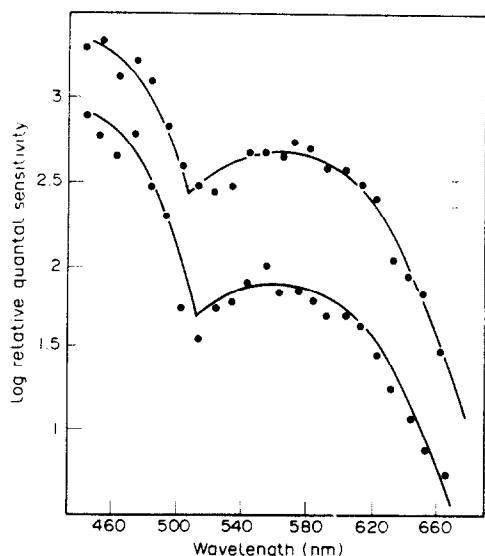


Fig. 2. Increment-threshold spectral sensitivity functions for two tree shrews. The functions for the two are arbitrarily positioned on the sensitivity axis. The vertical bar to the right indicates the size of the largest absolute difference in threshold at any of the test wavelengths for the two animals. The continuous lines were fit by eye (see text). Background luminance =  $5 \text{ cd/m}^{-2}$ .

sumed to represent performance at the brightness matches. It is noteworthy that each of these values is within 0.2–0.3 log unit of the brightness matches made by a normal human. As Fig. 1 clearly shows, there is a narrow band of wavelengths tree shrews cannot discriminate from an achromatic light, whereas wavelengths both

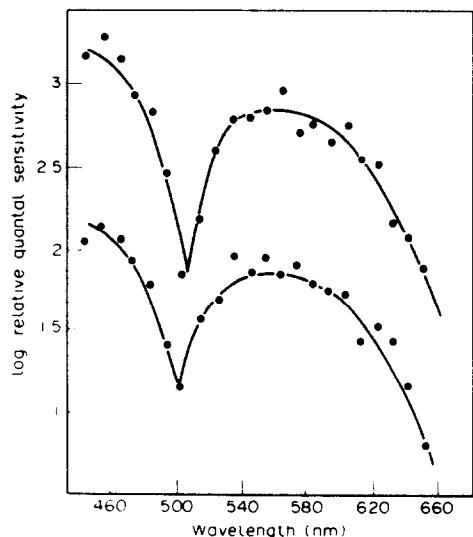


Fig. 3. Increment-threshold spectral sensitivity functions for two tree shrews. The functions for the two are arbitrarily positioned on the sensitivity axis. The continuous lines were fit by eye to the data points. Background luminance =  $25 \text{ cd/m}^{-2}$ .

longer and shorter are discriminable. We thus verify that *T. belangeri* has a spectral neutral point. The results for the two subjects are nearly identical. For each, performance fell below the 95% confidence level (dashed line in Fig. 1) over a range of 8–9 nm. The midpoint of this range was 504 nm for one subject, 505 nm for the other.

#### Increment threshold spectral sensitivity

Two complete spectral sensitivity functions were obtained from each subject for each adaptation condition. Figure 2 shows the second of these functions for each subject when the adaptation light was set to  $5 \text{ cd/m}^{-2}$ .

The functions are double peaked with high sensitivity at the shortest test wavelength (440 nm), a second peak at about 560 nm, and an intermediate region of low sensitivity in the range from 490–510 nm. The functions for the two subjects were similar. To illustrate this fact, the same template function has been drawn through the results for the two animals. The template was arbitrarily constructed by taking two wavelength-dependent visual pigment nomograms having  $\lambda_{\max}$  at 439 and 559 nm and individually sliding these two along the Y axis until they best fit the two components of this spectral sensitivity function. The only notable difference between the two subjects is the relative heights of the two components; the subject whose data are shown at the bottom of Fig. 2 having relatively higher sensitivity to the short wavelengths.

Figure 3 contains the spectral sensitivity functions obtained from the tree shrews at the higher adaptation level ( $25 \text{ cd/m}^{-2}$ ). As before, the threshold values are those obtained from the second complete runs on each animal. The functions for the two animals are again similar showing two clearly defined spectral components, one with a peak at about 440 nm and the other with a 550–560 nm peak. A striking difference between the functions obtained at the two adaptation levels is in the magnitude of the depression located between the two spectral peaks. At the higher adaptation level the trough of this depression is as much as a full log unit below the sensitivity values measured at the peaks.

#### Spectral sensitivity of the long-wavelength cone

The behavioral results make clear that the tree shrew retina must contain two classes of cone photopigments. We first sought to define

the spectral properties of the long wavelength member of this pair by recording the flicker photometric ERG under conditions which might be expected to maximize its contribution: high frequency flicker (62.5 Hz) and concurrent short-wavelength adaptation. The resulting spectral sensitivity functions obtained from five subjects (3 male, 2 female) are shown in Fig. 4. The solid circles are the corrected sensitivity values for each animal as determined at 10 nm intervals from 460 to 650 nm. The solid lines are the visual pigment nomograms which provided the best fit to each of the data sets. The nomograms provide excellent descriptions of these data. Shown on each function is the  $\lambda_{\max}$  value for that curve. These values cover a short spectral range—for five animals the average  $\lambda_{\max}$  value was 556 nm (SD = 0.71).

The close fits of the nomograms to the spectral sensitivity functions strongly suggests that these functions represent the operation of only a single cone class. We substantiated this conclusion by showing that it is impossible to produce any differential chromatic adaptation effects under these conditions of stimulation. To

accomplish this an ERG flicker photometric match was made between a 630 nm reference (0.11 mW) and a 540 nm test light. This match was then redetermined, alternatively in the presence of two steady chromatic adapting lights, 540 and 630 nm. The radiances of each of the latter were initially adjusted so that they each elevated the threshold of the 540 nm flickering light by about 0.5 log unit. The outcome was that the matches determined in the presence of the two chromatic adaptation conditions were not systematically different, were in fact usually identical. The conclusion is, thus, that the curves of Fig. 4 represent the outputs from only a single spectral mechanism.

#### *Spectral sensitivity of the short-wavelength cone*

The ease of isolation of signals from the long wavelength cone in the tree shrew with high frequency flicker is probably due to the fact that, as in other mammalian eyes (Zrenner, 1983), the short wavelength mechanism of the tree shrew has relatively low temporal resolution. No such reciprocal advantage exists to assist in the isolation of the short wavelength cone. The stimulus conditions used to measure the short wavelength cone with ERG flicker photometry were those determined in preliminary experiments to maximize its contribution, while at the same time minimizing the contribution from the long wavelength cone. These conditions included a slower flicker rate (25 Hz), a reference light to which the short wavelength cone should be particularly responsive (460 nm) and concurrent intense long wavelength adaptation. Even with all these advantages, and with the relatively large spectral separation between the long and short wavelength cones of the tree shrew, it is difficult, probably impossible, to completely eliminate any contribution from the long wavelength cone. Consequently, in examining spectral sensitivity under these conditions it was assumed that the derived function reflected some variable contribution from both the short and long wavelength cones. To determine the spectral position of the short wavelength cone we employed a computer routine in which the  $\lambda_{\max}$  value for one of the two contributors to the spectral sensitivity function was specified as 556 nm (Fig. 4) and the computer then searched to determine the  $\lambda_{\max}$  value of the second mechanism which when linearly summed with the 556 nm component provided the best fit to the spectral sensitivity function. The approach is

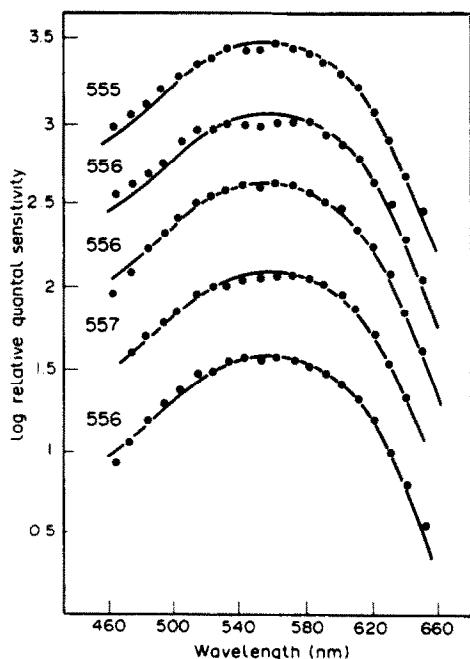


Fig. 4. Flicker photometric spectral sensitivity functions obtained from five tree shrews under conditions favorable for isolation of the long wavelength cone. The solid circles show sensitivity values obtained by equating the effectiveness of monochromatic test lights and an achromatic reference light. The solid lines are the best fitting visual pigment nomograms, the spectral peak of which is given for each animal. The curves have been arbitrarily positioned on the sensitivity axis.

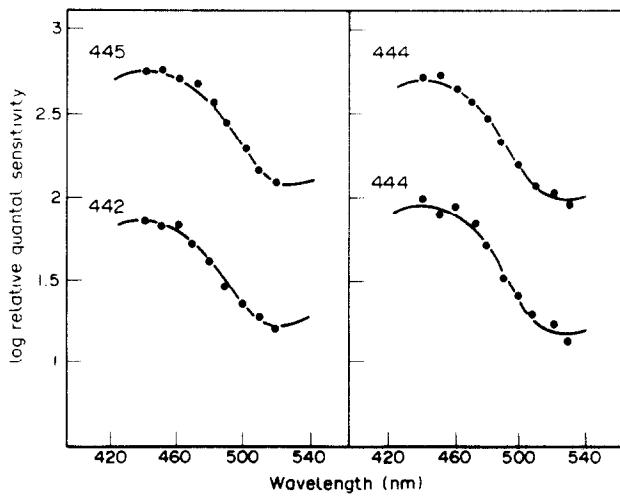


Fig. 5. Flicker photometric spectral sensitivity functions obtained from four tree shrews under conditions favoring contribution from the short wavelength mechanism. The continuous line is that for the best fitting linear summation of two nomogram pigment curves. In each, one of the components had a peak set to 556 nm. The wavelength peak of the short wavelength component required to complete the best fit is indicated on each curve. The curves for the individual animals are arbitrarily positioned on the sensitivity axis.

similar to that used in other ERG investigations (Nuboer *et al.*, 1983; Jacobs *et al.*, 1985). This procedure yielded the peak sensitivity (to the nearest nm) of the short wavelength pigment, the relative proportions of it and the 556 nm cone required to yield the best fit, and an index of the goodness of fit of the summed cones to the sensitivity data.

Figure 5 shows the spectral sensitivity functions obtained under these conditions for four tree shrews (2 male, 2 female). These conditions of adaptation and stimulation substantially isolated the short wavelength mechanism in the tree shrew. The proportion of the short wavelength component required to best fit the derived function varied only slightly among the four animals, from 78 to 85%. The  $\lambda_{\max}$  values of the short wavelength component required to complete the fit are indicated in Fig. 5. These values have relatively small individual variation with an average value of 443.8 nm (SD = 1.3).

## DISCUSSION

The outcome of the neutral point test confirms Polson's conclusion (1968) that the tree shrew is a dichromat. Although our test and hers were conducted with different achromatic standard lights and under somewhat different adaptation conditions, there is also close quantitative agreement between the neutral point locations she measured and those shown in Fig. 1. For five subjects Polson found an average

neutral point location of 505.5 nm; the corresponding value in the present experiment was 504.5 nm.

The ERG measurements appear to provide good estimates of the spectral mechanisms that account for tree shrew dichromacy. The peak sensitivity values obtained for the longer cone type, 556 nm, is not far from the average value reported by Tigges *et al.* (1967), and to the peak location suggested by results from behavioral tests involving discrimination of flickering lights (Polson, 1968). Determination of the spectral position of the short wavelength cone in the tree shrew necessarily depends on the adequacy of the estimate of filtering by the lens, and on the assumption that the ERG spectral sensitivity function can be accounted for by the linear addition of two spectral mechanisms having the shapes of nomogram photopigments. The first issue is probably not too serious since the lens corrections applied were relatively small (Tigges *et al.*, 1967). And any doubts about the reasonableness of the second assumption are moderated by the fact that it was possible to nearly isolate the short wavelength cone under the stimulus conditions used here. Coupled with the facts that the flicker photometric technique is highly reliable (Jacobs *et al.*, 1985), and that there were small individual variations in the estimates, it is reasonable to conclude that the short wavelength cone in the tree shrew peaks close to 444 nm. The spectral peaks estimated by the ERG procedure are similar to those recently

found for tree shrew cones as measured by microspectrophotometry (Petry and Harosi, personal communication).

If the cone spectral mechanisms in the tree shrew are those identified in Figs 4 and 5, then it should be possible to account for the behavioral spectral sensitivity results on the basis of their operation. The following represents an attempt to do this.

It has long been known that spectral sensitivity functions determined at increment threshold under conditions like those used here (i.e. large stimulus size, long duration) have multiple peaks which reflect the operation of spectrally opponent mechanisms (Sperling and Harwerth, 1971). King-Smith and Carden (1976) demonstrated that under conditions which produce these multiply-peaked functions in humans, the threshold for detection of the test light is the same as the threshold for determining the color of the light over most of the spectrum, thus providing further evidence that these spectral sensitivity functions depend on the operation of spectrally opponent neurons. The shapes of the spectral sensitivity functions obtained from the tree shrews imply spectral opponency. To see to what extent these functions could be accounted for entirely on the basis of simple spectral opponency, we used a computer to fit these functions using only subtractive combinations of the two spectral mechanisms ( $\lambda_{\text{max}} = 444, 556 \text{ nm}$ ). Figure 6 illustrates that this simple assumption yields a very good account of the thresholds actually obtained. The only obvious departure from the functions predicated solely on the basis of spectral opponency between these two mechanisms is where the signal from the opponent system goes to zero, i.e. in the vicinity of 500 nm. The failure to predict increment threshold in that region might be due to either or both of two factors: (1) the bandwidths of the monochromatic test lights were sufficiently broad that the signal from the spectrally opponent mechanisms was never nulled, (2) that in this region the test light increments were sufficiently high that they provided a usable signal to a nonopponent mechanism.

Polson (1968) earlier drew attention to a number of correspondences between the capacities of the tree shrew and those of human color defectives concluding that the tree shrew has deutanopic color vision. There are also a number of similarities between our results and those obtained from human deutanopes, including both the location of the neutral point

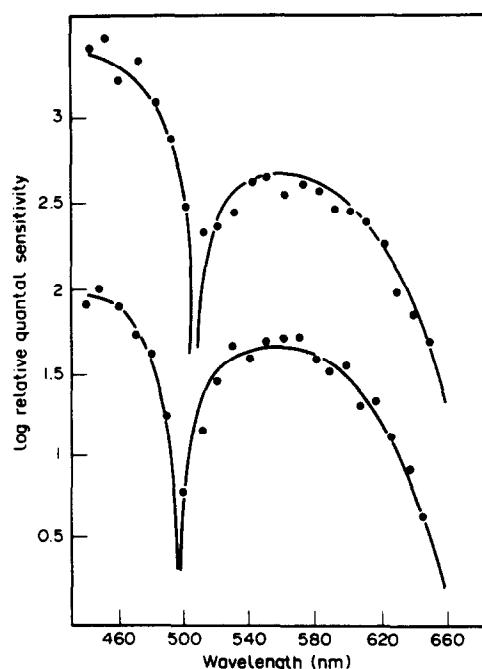


Fig. 6. Average increment threshold spectral sensitivity functions for two tree shrews. The values at the top were obtained when the background luminance was  $5 \text{ cd/m}^{-2}$ ; at the bottom the background luminance was  $25 \text{ cd/m}^{-2}$ . The continuous curves represent the best fitting subtractive combination of two nomogram pigments having  $\lambda_{\text{max}}$  of 444 and 556 nm. The proportions required for the best fits were: top (444 nm—84%, 556 nm—16%) and bottom (444 nm—69%, 556 nm—31%). The two functions are arbitrarily positioned on the sensitivity axis.

(Walls and Heath, 1956) and the appearance of the increment-threshold spectral sensitivity function (Zrenner, 1983). Although there have been many indirect estimates, to date there is only one report of direct measurement of the cone photopigments in human deutanopes. In a single subject whose retina was examined with the microspectrophotometer, Mollon *et al.* (1984) measured a long wavelength pigment having an average  $\lambda_{\text{max}}$  of 558 nm. That value is quite close to the present estimate of the peak of the tree shrew long wavelength pigment. It is much less clear how similar the short wavelength pigment of the tree shrew might be to that of human deutanope. One current estimate suggests that the short wavelength cone of the normal human (and presumably therefore also that of the deutanope) peaks at a significantly shorter wavelength (419 nm) than that of the tree shrew (Dartnall *et al.*, 1983).

There are also differences between human and tree shrew dichromacy. Increasingly it appears that in most cases human dichromacy exists only when the retinal region tested subtends  $2^\circ$

or less (Pokorny and Smith, 1982). Because the animals in this experiment were free to move about the test chamber it is not possible to accurately specify the retinal size of the stimuli, but observation of the animals suggests it unlikely that the fields ever subtended less than 30°. Thus tree shrew dichromacy is not restricted to relatively small sized targets. An additional clear difference between tree shrew color vision and human deutanopia is its genetic basis. Deutanopia has been argued to result from those relatively rare instances where individuals receive genes coding for the same middle to long wavelength cone pigments at two X-chromosome loci (or two loci on both X-chromosomes if the individual is female) (Piantanida, 1974). The genetics of color vision in the tree shrew are not known, but the fact that all of the subjects tested had identical dichromacies makes clear that the mode of inheritance must differ for tree shrew and human.

Irrespective of how closely the color vision of the tree shrew approximates that of the human deutanope, this animal does have a straightforward dichromacy uncomplicated by a great heterogeneity of retinal construction or by the presence of large numbers of rods often found in other dichromatic subjects. As such the tree shrew provides an attractive model for further investigations of dichromatic color vision.

**Acknowledgements**—We thank T. Geist and C. Lyon who assisted in the behavioral testing and M. Cognale who fabricated the ERG electrode. This research was supported by the National Eye Institute (EY-00105).

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