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CONE-BASED VISION OF RATS FOR ULTRAVIOLET AND VISIBLE LIGHTS

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Summary

Rats (*Rattus norvegicus*) have two classes of cone, one containing an ultraviolet (UV)-sensitive photopigment and the other housing a pigment maximally sensitive in the middle (M) wavelengths of the visible spectrum. The manner in which signals from these two cone types contribute to rat vision was investigated through recordings of a gross electrical potential (the electroretinogram, ERG) and behavioral discrimination tests. Spectral sensitivity functions obtained from both types of measurement indicate clear contributions from each of the cone classes, but there is a marked enhancement of the relative sensitivity to UV light in the behavioral index; for instance, under some photopic test conditions, rats are approximately equally sensitive to middle-wavelength and UV lights. In adaptation tests, thresholds for UV and M lights were found to be differentially elevated in the presence of chromatic adapting backgrounds, thus providing the possibility that signals from the two cones could be used by the rat visual system to support color discriminations. Evidence of dichromatic color vision in the rat was subsequently obtained from tests of wavelength discrimination.

Key words: rat, *Rattus norvegicus*, vision, cones, spectral sensitivity, color vision, ultraviolet sensitivity, electroretinogram.

Introduction

Daylight vision in vertebrates is initiated by the absorption of light by cone photopigments. Opsin genes from four families specify all the vertebrate cone pigments, but only two of these gene families are represented in mammals, where one yields all pigments absorbing in the short wavelengths (S) and the other provides pigments with maximum sensitivity in the middle-to-long wavelengths (Bowmaker, 1998; Yokoyama, 1994). The prototypical mammal thus has two types of cone photopigment, one drawn from each of these gene families. Two significant deviations from this pattern have been documented. First, mutations occurring in S-cone opsin genes reduce the retina of a number of mammalian species to a single cone type (Fasick et al., 1998; Jacobs et al., 1996a). Second, evolutionary changes that have occurred exclusively in the line to modern primates allow some of those species to acquire a third photopigment with peak sensitivity in the middle-to-long wavelengths (Jacobs, 1993). From many studied examples, there is a general expectation that the number of cone classes can be used to predict the character of the color vision an animal possesses.

Although vertebrates drawn from many groups have cone pigments with specific sensitivity in the ultraviolet (UV), for instance some birds, fishes, amphibians and reptiles, it was long believed that the absorption peaks of all mammalian short-wavelength cone pigments lay within the spectral range of approximately 415–450 nm (Goldsmith, 1994; Jacobs, 1992). About 10 years ago, however, it was discovered that the retinas of several common types of rodent (mice, rats, gophers, gerbils) contained photopigments with peak sensitivity well down into the UV range (Jacobs et al., 1991). Here, we report a series of measurements of visual sensitivity in rats. Of interest are the contributions of cone photopigments to vision in a nocturnal animal.

Cone pigments and cone representation in the rat

There is good agreement on the nature of the cone pigments of the rat. Measurements made with the electroretinogram (ERG) and behavioral tests indicate that one pigment has a peak at approximately 510 nm (Neitz and Jacobs, 1986), while spectrophotometric measurements made of pigment reconstituted in an artificial expression system give an equivalent value of 509 nm (Radlwimmer and Yokoyama, 1998). Hereafter, we refer to this as the M-cone pigment. Spectra measured in reconstituted photopigment gives a peak value for the rat UV pigment of 358 nm (Yokoyama et al., 1998), again in good agreement with earlier ERG measurements that yielded a peak at 359 nm (Deegan II and Jacobs, 1993). Template-based representations of the absorption spectra for pigments with peaks at 359 and 509 nm are shown in Fig. 1A. A limitation of the direct measurements of the M pigment is that they do not provide an account of the absorption of this pigment in the short wavelengths of the

precision necessary for studies of sensitivity in the UV. To predict that sensitivity, we assume in Fig. 1 that the spectral positioning and shape of the secondary absorption peak (β-band) of the M-cone pigment of the rat is like that suggested by direct electrophysiological measurements of cones in a cyprinid fish, *Danio aequipinnatus* (Palacios et al., 1996).

The rat is a strongly nocturnal animal with a rod-dominated retina, but it has long been known that the retina also contains cones (Walls, 1934). Photoreceptor counts in albino rats suggest that 1 % of the entire receptor complement is cones (LaVail, 1976; Szel and Rohlich, 1992). Opsin-specific antibodies have been used to label the two types of cone separately. In albino rats, application of this procedure indicated that approximately 7 % of all cones contain UV-sensitive photopigment (Szel and Rohlich, 1992). The present study used pigmented rats. To confirm that the receptor counts obtained from albino rats are also appropriate for pigmented animals, we used opsin antibody staining to obtain counts of the two cone types in the retinas of pigmented rats (Long–Evans strain.) The technique used for opsin antibody staining and cell counting has been described elsewhere (Calderone and Jacobs, 1999), and observations were made on three retinas. The density of cone photoreceptors varied from approximately 2000 mm^{-2} to 7000 mm^{-2} at different retinal locations. Among the cones, an antibody that detects UV cones labeled 11–12 % of the total. That value is in reasonable agreement with the earlier counts. Rats are thus similar to many other mammals in maintaining approximately an order of magnitude difference in the numbers of cones with maximum sensitivity in the short compared with the middle and long wavelengths (Szel et al., 1996).

The relative spectral sensitivities of rat cones can be derived from the estimates of the relative numbers of cones and photopigment spectral absorption. Fig. 1B shows the relative spectral sensitivity of the two types of rat cone, with the pigment spectra adjusted according to the proportions of the two cone types. These sensitivity curves suggest that rat M cones can potentially provide considerable sensitivity to light in the UV portion of the spectrum.

Materials and methods

Animals

Pigmented rats (*Rattus norvegicus*; Long–Evans strain) of both sexes were used. The animals, all young adults at the time of testing, were housed in individual cages and kept on a 12 h:12 h light:dark cycle with ambient illuminance having an average value of 20 lx. Animals that served as subjects in behavioral tests were deprived of food for 22 h before each test session.

Electrophysiological measurements

Indices of sensitivity in the outer retina were obtained from ERG recordings. Rats were anesthetized with an intramuscular injection of a mixture of xylazine hydrochloride (6.7 mg kg^{-1}) and ketamine hydrochloride (100 mg kg^{-1}), and the pupil was dilated by topical application of atropine sulfate (0.04 %). The sedated animal was placed in a head restraint. Body temperature was held at normal levels through the use of a circulating hot-water heating pad. Electrical signals were sensed from a bipolar contact-lens electrode.

The stimuli were delivered from a three-beam optical system, the output of which was presented in Maxwellian view as a circular field 57 ° in diameter. In these experiments, a single beam originating from a monochromator (10 nm half-bandpass) equipped with a 150 W xenon light source was used. A circular neutral density wedge was used to adjust the intensity of this light. The stimuli consisted of 12.5 Hz square-wave flicker presented with a duty cycle of 25 %.

The methods used to process ERG signals have been described (Jacobs et al., 1996b). In brief, analog hardware was used to window the amplified ERG signal with a sinusoid set to the frequency of the stimulus train (in this case, 12.5 Hz). This signal was viewed on a computer display screen. The responses were averaged for the last 50 of 70 stimulus cycles, and the resulting amplitudes were subsequently read directly

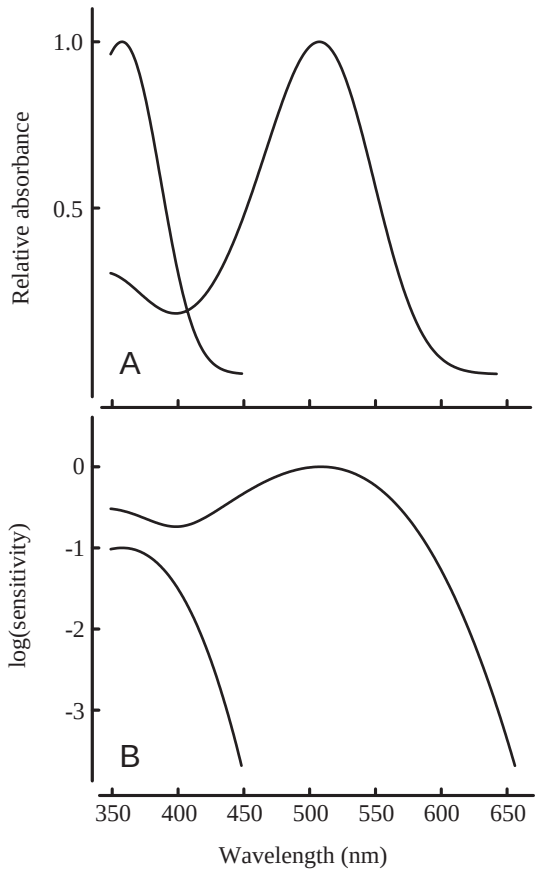

Fig. 1. (A) Template-based representations of the absorbance functions of two classes of cone found in the rat retina. The templates were derived for photopigments having peak absorbances of 359 nm and 509 nm (Palacios et al., 1996). (B) Relative spectral sensitivities for the two classes of rat cone. To derive relative spectral sensitivity, the absorbance functions at the top were scaled on the sensitivity axis to reflect the relative representation of the two cone types in the rat retina.

from a digital display. ERGs were recorded in a room illuminated with overhead fluorescent lights that yielded an ambient illuminance at the test eye of approximately 150 lx.

Behavioral measurements

Measurements of rat vision were made using standard operant procedures. Animals were trained in a three-alternative, forced-choice discrimination test using an apparatus described previously (Jacobs, 1983). Subjects viewed three small circular panels mounted along one wall of a test chamber. The rats were free to move about the test chamber and, depending on the position of the animal at the point where visual discriminations were made, the stimulus panels subtended visual angles that fell in the range from 14–60 °. The panels were transilluminated by an optical system located outside the test chamber. Illumination was provided by two sources, a grating monochromator with a 75 W xenon source (half-bandpass, 16 nm) and a tungsten–halide lamp. The former served as the test light that, through the use of a mirror system, could illuminate any one of the three panels and, depending on the aim of the experiment, light from the other source could be similarly directed so as to illuminate equally all three of the panels or any two of them. Each rat was trained to select the panel illuminated with the output from the monochromator and indicate its selection by touching that panel. Each correct response was reinforced by the automatic delivery of a 20 mg food pellet. The position of the test light was varied randomly across the three panels over successive trials. Test trials were signaled by the occurrence of a cueing tone and terminated when the animal responded, or after 4 s without a response. Over trials, the intensity and spectral content of the test light were varied to permit the determination of threshold performance. Trained animals completed 300–600 test trials in each daily session. All aspects of stimulus presentation, reinforcement delivery and response monitoring were accomplished under the control of a laboratory computer. Ceiling-mounted fluorescent tubes were used to illuminate the test chamber (ambient illuminance 70 lx).

Results

ERG spectral sensitivity

Spectral sensitivity functions were measured by iteratively adjusting the intensity of a monochromatic test light flickering at 12.5 Hz to produce an ERG with amplitude of 3.2 μV. Thresholds were measured for test lights taken at 10 nm intervals from 360 to 590 nm. The entire process was repeated, and the two threshold values were subsequently averaged. The deviations between the two threshold values were small, on average less than 0.1 log unit. The averaged functions obtained from three animals are shown in Fig. 2. Here and in the subsequent spectral sensitivity functions, the sensitivity values have been corrected for absorbance by the rat lens (Gorgels and van Norren, 1992). We determined the best summative fit of the cone template functions from Fig. 1 to these sensitivity data. The combination of 359 nm (17 %) + 509 nm (83 %) provides that fit (solid line in Fig. 2) and accounts well for the ERG spectral sensitivity function.

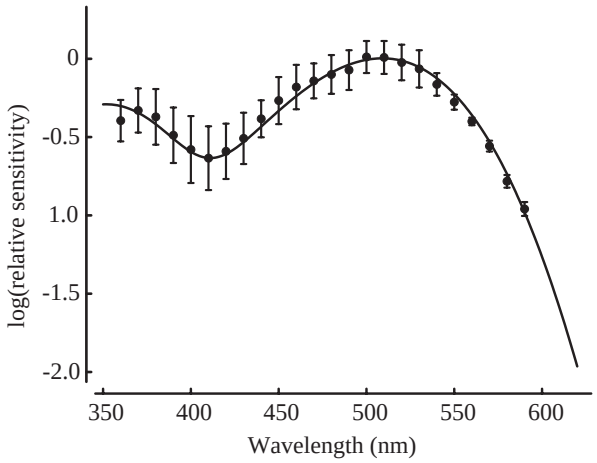

Fig. 2. Rat electroretinogram spectral sensitivity function obtained for 12.5 Hz flicker using an amplitude criterion of 3.2 μV. The filled circles are mean values for three animals (±1 S.E.M.). The continuous line represents the best-fitting linear summation of the two cone-pigment template curves from Fig. 1 (see text).

Behavioral spectral sensitivity

Increment-threshold spectral sensitivity was measured for three female rats. To accomplish this, the three panels were continuously illuminated with an achromatic light (6200 K; log(luminance)=1.12, where luminance is measured in cd m^{-2}). Thresholds were measured for monochromatic test lights taken at 10 nm intervals from 360 to 610 nm. At each wavelength, the intensity of the monochromatic light was varied in steps of 0.3 log unit, with a range of intensities pre-selected so as to produce discrimination performance that varied from approximately 90 % correct down to chance performance. Wavelengths were tested in random order, and the testing was continued over a series of daily sessions until at least 100 trials had been accumulated at each intensity/wavelength combination. From these results, psychometric functions were constructed by fitting these performance data to a logistic function having asymptotes of 100 and 33 % correct, with the variance and mean value as free parameters. The function providing the best least-squares fit was determined, and threshold was taken as the intensity of the stimulus that yielded discrimination performance at the upper 99 % confidence level. The sensitivity values (means ± 1 S.D.) for three animals are shown in Fig. 3. These sensitivity measurements have been fitted in the same fashion as the ERG data, i.e. by determining the best additive fit of the cone template functions. The solid line shows the best fit, obtained for the combination of 359 nm (42 %) + 509 nm (58 %).

For one rat, we subsequently used the same techniques to measure complete spectral sensitivity functions at three additional background light levels [log(luminance)=1.43, 1.76 and 2.09]. Fig. 4 shows these functions. Each of the three has been fitted using summative combinations of the 359 nm and

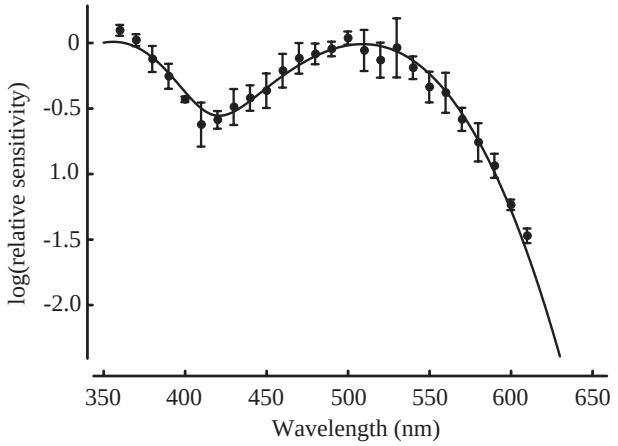

Fig. 3. Increment-threshold spectral sensitivity functions for the rat. The thresholds are mean values (±1 S.D.) for three subjects as measured on an achromatic background [log(luminance)=1.12, where luminance is measured in cd m^{-2}]. The curve is the best-fitting linear summation of the cone pigment templates.

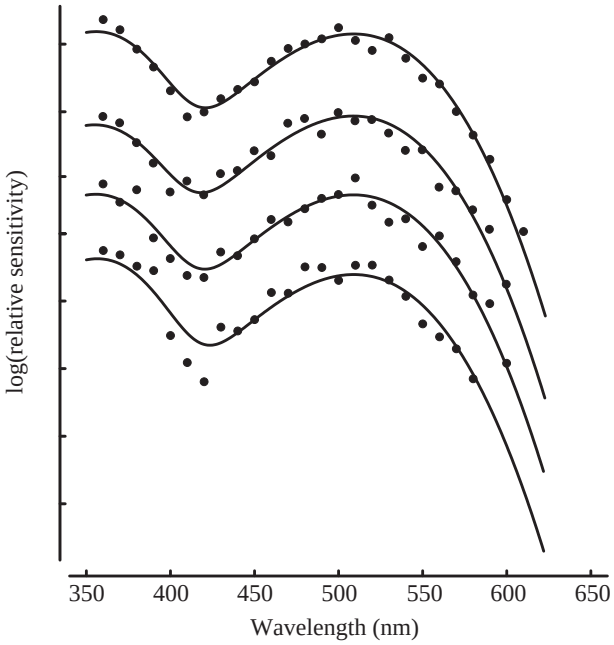

Fig. 4. Rat increment-threshold spectral sensitivity functions for four different achromatic backgrounds [from top to bottom: log(luminance=1.12, 1.43, 1.76 and 2.09, where luminance is measured in cd m^{-2}]. The top curve is a replot of the mean results from Fig. 3 and below that are spectral sensitivity functions obtained from an animal tested on three backgrounds that were progressively elevated in luminance. Each scale division on the sensitivity axis is equal to 0.5 log unit. The four spectral sensitivity functions have been best fitted with linear summations of the cone templates. The percentage of the 509 nm component required in these best fits is (from top to bottom): 58 %, 64 %, 58 %, 49 %.

509 nm cone templates. The functions are accurately positioned on the sensitivity axis, and it can be seen that adaptation produces an intensity-dependent loss of sensitivity all the way across the spectrum. Although there is some variation in the shape of the spectral sensitivity functions obtained for different adaptation states, it is not obvious that there is any systematic change in the relative amounts of the 359 nm and 509 nm components required to best fit the function. To evaluate that possibility, a linear regression was obtained for the proportion of the 509 nm component plotted against the four background light levels. The slope of the line was not significantly different from zero (t=1.291; d.f.=2). The absence of a systematic change in spectral sensitivity is perhaps surprising since, although the background light has been characterized as 'achromatic', it actually had relatively greater energy throughout the visible spectrum than in the UV region. Consequently, one might have expected that it would have reduced the contribution from the cones containing M pigment to a greater extent than that from the UV cones. Additional measurements were undertaken to study more selectively the effects of light adaptation on rat visual sensitivity.

Effects of chromatic light adaptation

To determine whether the adaptive effects of light on rat behavior are spectrally univariant, we measured increment thresholds for two test lights (390 nm and 510 nm) on a 560 nm background. The latter wavelength, 560 nm, should produce no significant response in rat UV cones. To ensure that these measurements reflected contributions from cone signals, the intensity of the 560 nm background light was first adjusted to a level that yielded approximately the same threshold sensitivity values as are represented in the photopic spectral sensitivity function of Fig. 3. Thresholds were then measured for 390 nm and 510 nm test lights for background light levels that were progressively increased (in steps of approximately 0.2 log unit) from this value to the brightest obtainable in the test apparatus. Each threshold was measured as described above, and 33 separate threshold measurements were obtained from three rats.

As suggested by the previous experiment, long-wavelength light adaptation indeed produces a significant threshold elevation for UV test lights. The results from this experiment are summarized in Fig. 5, in which the threshold elevation for the 390 nm test light is plotted against the threshold elevation for the 510 nm test light for all of the subjects at each of the background light levels. The continuous line is the best-fitting linear regression (slope=0.71; r^2=0.93, P<0.001). The broken line in Fig. 5 predicts what would be expected if the two pigments adapted in a univariant fashion. That prediction differs significantly (P<0.01) from the threshold elevation data actually obtained.

Spectral discriminations

The presence of two classes of cone, and evidence that signals originating in the two do not behave in a strict univariant fashion in a behavioral discrimination test (Fig. 5), suggest that the rat might have a visual system organization that could support some color vision. This possibility was

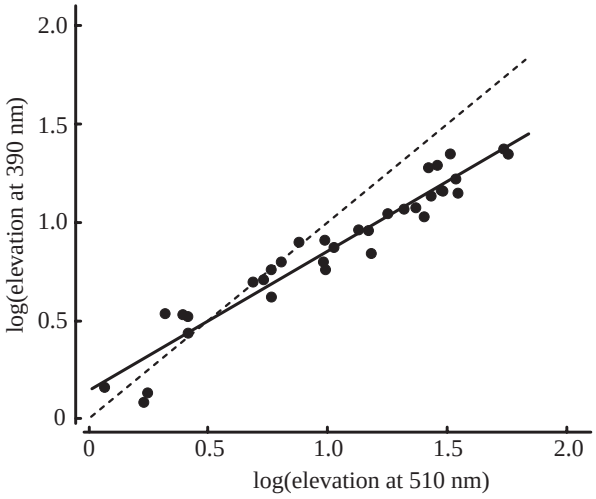

Fig. 5. Effects of chromatic adaptation on visual thresholds in the rat. Increment thresholds for two test lights (510 nm and 390 nm) were measured on 560 nm backgrounds of various intensities. Each plotted point is a comparison of the elevation in threshold produced for the two test wavelengths at a single background light intensity. Results are shown for three subjects. The straight line is the best-fitting linear regression (slope=0.71, r^2=0.93, P<0.001). The broken line shows the relationship between the threshold elevations for the two test wavelengths expected if the two cone mechanisms had adapted univariantly.

examined by determining whether rats could discriminate between visible and UV light. Three animals (two females, one male) were tested. Tests of color discrimination require that brightness cues be controlled. We used a technique to establish brightness matches between different spectral stimuli similar to that employed in earlier studies of mice (Jacobs et al., 1999). Each of the subjects was first trained to make brightness discriminations. With that skill acquired, they were presented with a discrimination between a very bright 510 nm test light and two dimmer panels having the same spectral content as the test light (510 nm). Then, over trials, the intensity of the 510 nm test light was progressively dimmed in steps of 0.1 log unit. When the test light was much brighter than the comparison lights, the animals selected it consistently, but as the intensity of light was dimmed the percentage of correct selections declined, eventually reaching chance levels. With still further decreases in the intensity of the test light, the animals began actively to avoid the test light, presumably because the other two panels now appeared brighter than the test light. The intensity of the test light yielding chance performance was taken as the point of equal brightness between the test and comparison lights. A similar brightness match was made between the light from the monochromator set to a value of 370 nm, and a comparison produced by passing light from the tungsten–halide lamp through a Schott UG-1 filter. Spectroradiometric measurements of the test panels illuminated with this light had peak radiance at 370 nm (half-width=30 nm). With these two brightness matches established, matches for various wavelength combinations could be readily calculated on the basis of the spectral sensitivity functions already determined. The adequacy of this technique as a means for controlling brightness cues is illustrated below.

We first tested animals to determine whether they could discriminate monochromatic test lights from a UV light (produced as described above.) The test light was set to 510 nm, and over trials it was presented at the intensity value computed to be equally bright to the UV light and at intensity values that were randomly varied over a range of ±0.6 log unit in steps of 0.1 log unit from the point of the brightness equation. Following an extensive training period, all three subjects were eventually able successfully to discriminate 510 nm light from UV light over the entire range of test light intensities. The wavelength of the test light was then progressively changed in steps of 10 nm towards the shorter wavelengths. At each wavelength, the test light was presented at intensity values calculated to be equally bright to the test light and over the additional intensity range indicated above. The asymptotic discrimination performance for the three subjects achieved at the equal brightness settings is shown in Fig. 6. Each successfully discriminated between the test light and the UV stimulus until the wavelength of the former was shortened to approximately 400 nm. For wavelengths shorter than 400 nm, none of the animals showed successful discrimination. In a second test, the direction of the discrimination was reversed, i.e. rats were now trained to select a monochromatic UV test light (370 nm) from a 510 nm light (10 nm half-bandwidth). Controls for brightness cues were instituted in the same fashion as described above. Once this discrimination had been acquired the test light was stepped towards longer wavelengths. The results are also summarized

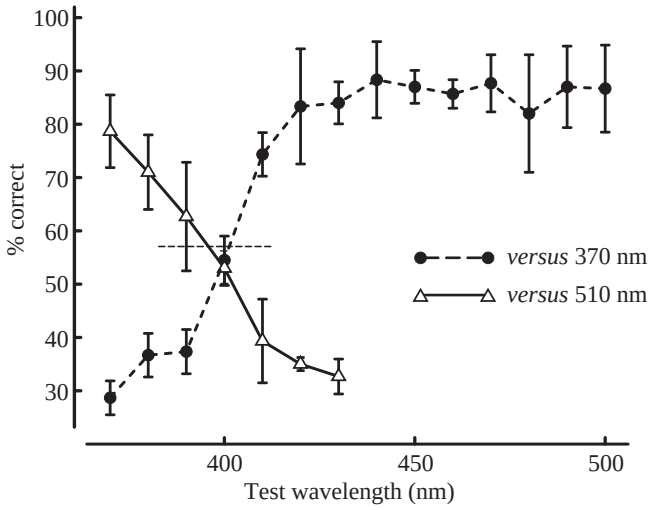

Fig. 6. Results from tests of wavelength discrimination by rats. The plotted points are the mean performance achieved by three rats (± 1 S.E.M.) for various test wavelengths *versus* a 370 nm light (circles and broken line) and for various test wavelengths *versus* a 510 nm light (triangles and solid line). The performance data are for pairs of lights that have been equated to be equally bright for the rat. The horizontal dashed line indicates chance performance for the number of test trials that were run.

in Fig. 6, in which it can be seen that the subjects could successfully discriminate UV light from the 510 nm light until the wavelength of the test light was set to approximately 400 nm. For wavelengths longer than 400 nm, color discrimination failed.

The results shown in Fig. 6 document color discriminations of the type expected of a subject having two classes of cone pigment with spectral properties like those found in the rat retina. A substantial period of training and testing was required to produce these results, and a concern is that the rats may simply have eventually learned to exploit some subtle brightness cue. Fig. 7 provides evidence that this was not the case. Fig. 7 summarizes the results obtained from a rat that was required to discriminate two test lights, 380 nm and 510 nm, from a 510 nm light. The cumulated performance over 100 test trials for each wavelength over the full range of intensity variation is shown. Note that, for 510 nm *versus* 510 nm, the animal successfully discriminates stimuli both brighter and dimmer than those calculated to be equally bright, but fails to discriminate between the two lights when brightness differences have been removed. The deviations from the equal brightness settings required for successful discrimination amount to less than 0.2 log unit. In contrast, the rat successfully discriminates between 380 nm and 510 nm lights at the point of calculated brightness as well as for all values both above and below this. It seems clear that potential brightness cues were adequately controlled in this test. Note that, although this animal can make a purely spectral discrimination between 380 nm and 510 nm, it nevertheless discriminates better when there are both spectral and brightness cues present than when there are only spectral cues.

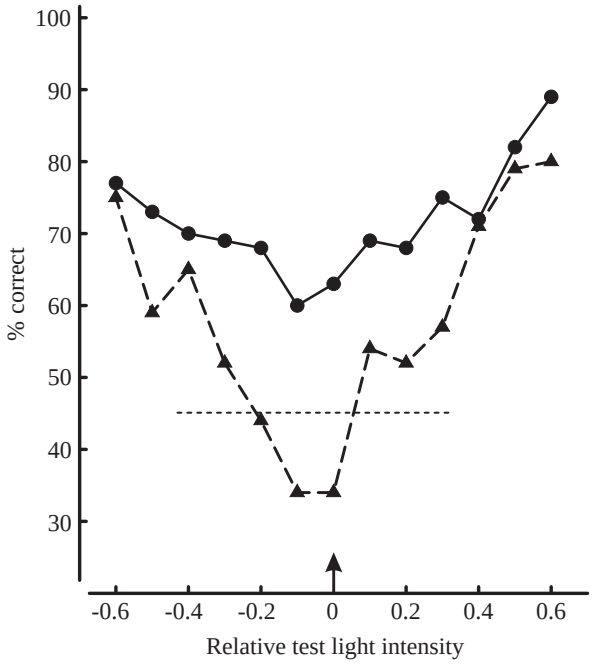

Fig. 7. An illustration of the effectiveness of the brightness controls used in the test of rat color vision. In successive experiments, a rat was required to discriminate between a test light of either 380 nm or 510 nm and a 510 nm comparison light. Each of the test lights was presented an equal number of times at an intensity that had been predetermined by the brightness equation procedure (see text) to be equally bright (arrow) to the comparison light as well as for values brighter (positive) or dimmer (negative) than the comparison light. Intensities are plotted in logarithmic units relative to the brightness match, and each plotted point shows performance over a total of 100 test trials. The broken line indicates the 99 % confidence level. Note that the animal always successfully discriminates between 380 nm and 510 nm lights, but fails to discriminate between the 510 nm test and comparison lights when the brightness cues are eliminated.

Discussion

Because their retinas typically contain only a relatively small population of cones, it is difficult to study the nature of cone-based vision in nocturnal mammals. In rodents such as the rat, that difficulty has been compounded because one of the cone types in these animals is effectively blind to the stimuli that have classically been employed in vision experiments. The observations presented here document some features of cone-based vision in rats, showing that they can readily detect UV light in laboratory experiments and can use signals from their two cone classes to support rudimentary color discrimination.

Rat cone vision and the rat visual system

Signals from rodent UV cones were first detected in ERG measurements, and their spectra were assessed by recording ERG responses in the presence of intense long-wavelength adaptation (Jacobs et al., 1991). Under those conditions, UV-cone signals are prominent in the ERG. However, in spectral sensitivity measurements made in the absence of chromatic adaptation, the contribution of UV cones to ERG signals is modest (Fig. 2). ERGs obtained for flickering lights are interpreted as reflecting some combination of photoreceptor and bipolar cell signals (Bush and Sieving, 1996). As judged by the cone template fits, the relative contributions from rat UV- and M-cone types to the ERG flicker signal are not far from what would be predicted if the two cone classes simply contribute to the signal in accord with their relative numbers. The picture is quite different for the increment-threshold behavioral measurements (Fig. 3, Fig. 4) where the template fits suggest a 40–50 % relative contribution from the UV cones as opposed to around 17 % in the ERG signal. Somewhere beyond the outer retina, there is a clear enhancement in the relative strength of the UV cone signals.

Recent work makes it clear that, with the exception of the primate fovea, there is considerable commonality of structural organization in the retinas of all mammals (Boycott and Wassle, 1999; Jeon et al., 1998). For instance, it has been noted that the density of cones in a number of mammalian retinas (including the rat) is similar to that found in the peripheral retina of primates (Boycott and Wassle, 1999). There are perhaps ten discrete and structurally analogous classes of bipolar cell in both rat and primate retina. In the monkey, nine of these are believed to transmit cone signals to the inner retina (Boycott and Wassle, 1999) and, with one exception, all of

them appear to be connected to middle-wavelength-sensitive (M) or long-wavelength-sensitive (L) cones or to both these cone types. The analogous bipolar cells of the rat retina probably, therefore, contact the M cones. The primate retina also contains a class of bipolar cell that selectively contacts S cones and transfers these signals to the inner plexiform layer. Again, structurally similar cells are found in the rat retina, and it seems reasonable to suppose that they transmit signals originating in the UV cones. The greater prominence of the UV-cone signal seen in behavioral measurements probably reflects differential gain mechanisms for UV- and M-cone signals. The comparison of ERG and behavioral spectra suggests that these gains could be applied at locations in the inner retina or deeper in the visual system.

Fig. 6 illustrates the fact that rats can be trained to perform dichromatic color discriminations. At least for mammals, this would ordinarily be interpreted to imply the presence of spectral opponent mechanisms in the visual system. We are not aware of any results from electrophysiological experiments that document the presence of such cells in rats. However, the cone photopigments of the mouse retina are nearly identical to those of the rat, and it has been reported that approximately 12 % of mouse ganglion cells receiving cone signals manifest opponent responses for UV- and M-cone inputs (Ekesten et al., 2000). Interestingly, these authors also detected ganglion cells that receive cone inputs exclusively from UV cones. Depending on the nature of their central connections, either or both of these classes of ganglion cell could contribute information useful for color discriminations. However, even though their cone pigments are similar, there are sufficient differences to suggest that the mouse may not provide a good model for the processing of cone information in the rat. These differences include the facts that: (i) the mouse has relatively more cones than the rat (3 % *versus* 1 %) and UV cones outnumber M cones (Szel et al., 1996), (ii) unlike the rat, the spatial distribution of the two cone types is very heterogeneous in the mouse, with M cones completely absent from the ventral retina (Szel et al., 1992), and (iii) some proportion of mouse cones coexpress UV and M pigments (Pugh et al., 1998), while coexpression has not been observed in rat cones (Szel et al., 2000). While it seems likely that some rat ganglion cells have a spectrally opponent organization, the scarcity of rat UV cones suggests that the numbers of such cells may be quite small.

The utility of rat cone vision

These laboratory measurements document what rats can accomplish using cone-based vision with reasonably high light levels, but by their nature say little about how this might translate into seeing under natural circumstances. What is clear from the spectral sensitivity measurements is that, for at least some viewing conditions, rats maintain reasonable visual sensitivity into the UV portion of the spectrum, about equal in fact to their sensitivity to middle-wavelength light. How useful that might be obviously depends on the availability of short-wavelength light. Measurements made in natural habitats indicate a number of environmental circumstances in which, during daylight hours, there is relatively abundant UV radiation (Endler, 1993) and, interestingly, there is a significant increase in the ratio of 360 nm:520 nm light coming from the sky during the morning and evening twilight hours (Hut et al., 2000). High UV sensitivity would seem likely to be advantageous under those conditions. Rats, however, are nocturnal and, under scotopic conditions, any advantages of UV photoreceptors disappear.

Whether the abilities of rats to make some color discriminations have a practical utility is also unclear. Blue skylight is a particularly rich source of UV irradiance and predominantly long-wavelength targets appearing against such a background, for instance a bird of prey, might provide a circumstance where this color capacity could be usefully employed (although birds may also have evolved countermeasures; Rowe, 1999). As mentioned above, we found training rats to make color discriminations a challenging task. Specifically, a very large number of training trials were required before the animals could be encouraged to discriminate on the basis of spectral differences rather than brightness differences. The difficulty of providing a demonstration of color vision might reflect the fact that the operant task we employed was not an optimal one, or it may be that color differences normally have only a weak cue value for rat vision. Discriminations involving more naturalistic stimuli might be used to evaluate this possibility.

Finally, in recent years, there have been a number of experiments on the role of UV light in the mammalian circadian system (Amir and Robinson, 1995; Brainard et al., 1994; Hut et al., 2000; Provencio and Foster, 1995). The presence of UV cones in some rodents might well mediate the effects of light on circadian systems. However, UV light entrainment of circadian rhythms is possible even in species that lack a population of UV cones. For example, the Syrian hamster has no UV cones (Calderone and Jacobs, 1999), but can still be entrained to UV light (Hut et al., 2000; von Schantz et al., 1997). The pigment spectra of Fig. 1 suggest that the relatively high absorption by the β-bands of pigments whose primary peaks are around 500 nm (which includes both rods and M cones for most rodents) probably provides the initial source of the entrainment signal for rodents lacking UV photopigments.

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