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Research Note

Spectral sensitivity of cat cones to rapid flicker*

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Summary. Records obtained from the flicker photometric electroretinogram indicate that only a single spectral mechanism (λ_{MAX} = 555 nm) in the cat eye contributes to the response to 50 Hz flicker. A photopic mechanism (λ_{MAX} = 500–510 nm) detected in earlier studies does not respond to high frequency flicker.

Key words: Cat cones – Spectral mechanisms – Flicker photometry

Introduction

Although there are exceptions (Saunders 1977), most studies of spectral mechanisms in the cat visual system have found good evidence for the presence of two classes of cone having maximum sensitivity at 445–455 nm and 550–560 nm respectively (Daw and Pearlman 1970; Crocker et al. 1980; Schuurmans and Zrenner 1981; Wienrich and Zrenner 1983). The presence of a third spectral mechanism, recorded under conditions which should greatly disadvantage rod contributions, has also been detected (Crocker et al. 1980; Wienrich and Zrenner 1983). This mechanism has a spectral peak at 500 to 510 nm; on various grounds it has been concluded that it is a photopic mechanism, perhaps a third class of cone. In the course of using the flicker photometric electroretinogram (ERG) to examine cone spectra in a number of different species we have made observations on the nature of the spectral mechanisms responding to high frequency flicker in the cat eye. These indicate that the 500–510 nm mechanism is, at the least, not a typical mammalian cone.

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Material and methods

Adult domestic cats (*Felis cattus*) of both sexes were used. They were anesthetized (20 mg.kg^{-1} of ketamine hydrochloride plus acepromazine maleate followed by 10 mg.kg^{-1} of sodium pentobarbital) and received atropine sulfate to inhibit mucus secretions. The pupil of one eye was dilated by topical application of atropine sulfate and Phenylephredine HCl. The animal was placed in a modified stereotaxic instrument in which the head is supported and positioned by adjustment of several large neoprene pads. Normal body temperature was maintained during the experiment through the use of a circulating hot water heater. The ERG was recorded with a bipolar contact lens electrode.

The apparatus and procedure for recording flicker photometric ERGs have been fully described (Neitz and Jacobs 1984). Stimuli are produced by a three-beam Maxwellian-view optical system. One beam serves as the test light, the second as the reference, and the third can be used for accessory adaptation. All are optically combined to illuminate a 53 deg patch of the retina. As in classical flicker photometry, the intensity of the test light is adjusted at each of a series of wavelengths so as to be equally effective to the constant reference light. In these experiments the test light was from a monochromator (half-energy passband = 10 nm). The reference light was achromatic (corneal radiance = 0.11 mW). The ERGs elicited by alternating flashes from the test and reference light were passed through active narrow bandpass filters and subtracted one from another. A photometric equation was established by positioning a density wedge to adjust the intensity of the test light until it just nulled the response to the reference light. It has been previously shown that this provides a sensitive, reliable, and valid way to make spectral sensitivity measurements (Neitz and Jacobs 1984). For each animal photometric equations were obtained for monochromatic lights taken at 10 nm steps over the range from 460 to 630 nm. Equations were also made in the presence of intense chromatic adapting lights (see below). All the recording was done in a lighted room; thus the test eye was always ambiently light adapted (retinal illuminance = 4.14 log td.) in addition to whatever light adaptation was provided by the conditions of the experiment.

To construct spectral sensitivity functions, the wedge settings at each test wavelength were appropriately corrected and compared to wavelength-dependent visual pigment nomograms (Dawis 1981). A computer was used to determine the spectral position (to the nearest nm) of the nomogram giving the best fit to the array of sensitivity measurements. To accomplish this, the difference squared between each sensitivity value and a nomogram was computed for every possible nomogram. The nomogram

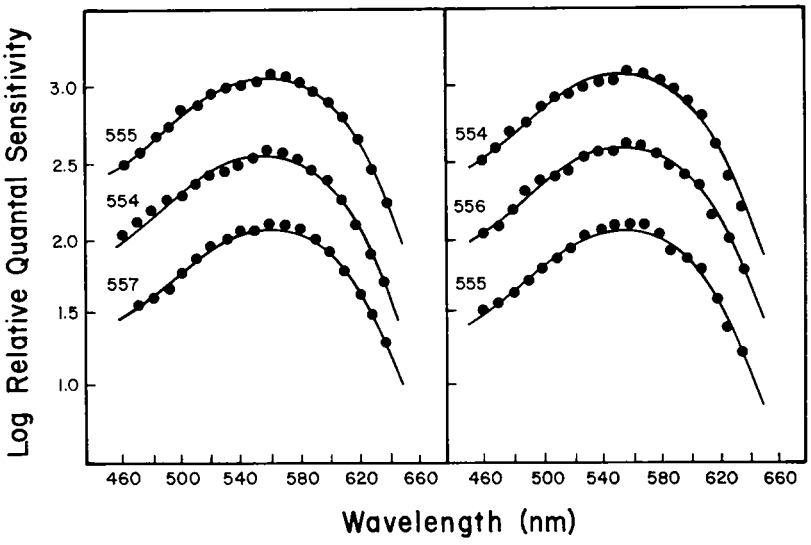

Fig. 1. Flicker photometric spectral sensitivity functions for six cats. The solid circles are sensitivity values obtained by equating the effectiveness of flickering monochromatic test lights and an achromatic reference light. The solid lines are the best fitting visual pigment nomograms; the peak for each is indicated on the curve. The functions are arbitrarily positioned on the sensitivity axis. Flicker rate: 50 Hz

which produced the smallest average difference squared was selected as best fitting the data.

Results and discussion

Complete spectral sensitivity functions were obtained from six cats (5 male, 1 female) using 50 Hz flicker. The functions (Fig. 1) are simple in form and extremely well fit by curves generated from single pigment nomograms. The spectral peaks of these best fit curves cover a short range, from 554 to 557 nm.

The obvious lack of any systematic departures from the nomogram curves of the data shown in Fig. 1 suggests that for 50 Hz flicker only a single class of cat cones contributes to the ERG. A further test of this conclusion was to see if intense chromatic adaptation altered the spectral sensitivity functions, as would be expected if more than a single spectral mechanism contributed to the curves of Fig. 1. For this purpose a 50 Hz photometric equation was made between a 510 nm test light and a 630 nm reference light. These equations were made, alternately, in the presence of steady chromatic adaptation of 510 nm and 630 nm. These particular wavelengths were selected because one (510 nm) would be expected to be relatively much more effective at adapting a 510 nm mechanism than a 555 nm mechanism; the other adaptation light (630 nm) should have the reverse effect. The intensities of the chromatic adaptation lights were initially adjusted so that each elevated the threshold for obtaining a criterion (2 μV) response to the 510 nm flicker by an additional 0.6 log unit. The results of this experiment were clear and consistent: in no individual case was there ever any systematic shift in the photometric equations associated with a change in the chromatic adaptation state of the eye. These equations can be routinely made to an accuracy of 0.05 log units or better (Neitz and Jacobs 1984), and thus any chromatic adaptation effect of that magnitude or larger would have been detected. For purposes of comparison identical tests were run on rhesus monkeys (*Macaca mulatta*), a species in which the two relevant cone types are spectrally separated by only about one half the distance of the cat 510 and 555 nm spectral mechanisms. Here the same procedure yielded systematic threshold shifts on the order of 0.15 to 0.20 log unit.

The conclusion from these experiments is that only a single spectral mechanism contributes to the response to 50 Hz flicker in the cat eye. The short wavelength cone mechanism in the cat has low temporal responsivity (Zrenner and Gouras 1979) and thus its lack of contribution to the 50 Hz flicker response was expected. The mechanism that does respond to 50 Hz flicker behaves univariantly. The conventional interpretation of this fact is that only a single spectral mechanism must contribute to the response (Rushton 1972). In addition, the shape of the spectral sensitivity function (Fig. 1) is appropriate to the operation of a single cone class. The average spectral peak for this mechanism for six animals was 555.2 nm (SD = 1.17), a value closely compatible with the peak location claimed for the cat long cone in most of the earlier studies noted above.

The 510 nm mechanism in the cat provides no contribution to the ERG response to rapid flicker. A number of other types of middle to long wavelength mammalian cone mechanisms have now been tested with the flicker photometric ERG under conditions

identical to those of the present experiment. All have been found to respond under such conditions (Jacobs and Neitz 1985). In fact, this result holds for other cones which also show peak sensitivity at about 510 nm; for example, those found in the retina of the rat (Neitz and Jacobs 1986). The absence of contribution of the 510 nm mechanism in the cat under such stimulus conditions leads us to suggest that, either, (a) the 510 nm mechanism in the cat is a cone whose temporal response properties are more like those of short wavelength cones than typical middle or long wavelength cones, or (b) the 510 nm mechanism is not a cone, but rather reflects rod contributions. Various evidences have been presented against the latter possibility (Crocker et al. 1980; Weinrich and Zrenner 1983). However, in an eye with a very large rod complement, like that of the cat (Steinberg et al. 1973), it is extremely difficult to be certain that all contribution from the entire population of rods has been obviated through the use of steady adaptation lights. Whatever its basis might be, it is noteworthy that a recent behavioral study of spectral sensitivity in the cat yielded no evidence that a 510 nm mechanism contributes to performance under photopic conditions of adaptation (Loop and Millican 1984). Rather, under those conditions, visual behavior appears entirely dependent on information from the 450 and 556 nm cone types. Taken together, that result and the present experiment make it increasingly unlikely that the cat could have trichromatic color vision.

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