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PHOTOPIC SPECTRAL SENSITIVITY OF THE CAT

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SUMMARY

1. The psychophysical spectral sensitivity of cats was assessed using a two-choice visual discrimination task by determining increment thresholds and critical flicker frequency on white and chromatic backgrounds.

2. For large increments, on 0·0, 0·3 and 3·0 cd/m^2 white backgrounds, the cats were most sensitive to 497 nm indicating that these backgrounds are scotopic. On 30 and 300 cd/m^2 white backgrounds, the cats were most sensitive to about 454 and 561 nm indicating that these backgrounds are photopic. Sensitivity to intermediate wave-lengths indicated independent action of 'blue' and 'green' cones.

3. For large increments, thresholds on photopic yellow and magenta backgrounds indicated the additive influence of 'blue' and 'green' cones.

4. Spectral sensitivity functions obtained with a critical flicker frequency criterion of 10 Hz on a 30 cd/m^2 white background reflected only the activity of the 'green' cone while at 20 Hz the function reflected an additive contribution of both 'blue' and 'green' cones.

5. For small increments, on a 30 cd/m^2 white or 96 cd/m^2 orange background, sensitivity reflected only the activity of the 'green' cone.

6. The cat's photopic spectral sensitivity is influenced by the psychophysical test upon which it is based in a manner that is similar to what has been found for other vertebrates. No evidence was found for a 500 nm mechanism active at photopic levels.

INTRODUCTION

Although the visual system of the cat has been extensively studied the number of cone types the cat possesses remains contentious. While neurophysiological evidence for green-sensitive (560 nm) and blue-sensitive (455 nm) cones is clear (Hammond, 1978), there is little agreement on the relative influence of blue-sensitive cones: some workers find 'blue'-cone influence to be rare (Daw & Pearlman, 1969, 1970; Hammond, 1978) while others find it to be common (Crocker, Ringo, Wolbarsht & Wagner, 1980; Schuurmans, 1981). Recently several studies have concluded that the cat is a photopic trichromate having, in addition to 'green' and 'blue' cones, a cone whose sensitivity peaks at around 500 nm (Ringo, Wolbarsht, Wagner, Crocker & Amthor, 1977; Schuurmans, 1981; Zrenner & Wienrich, 1981) or a red-sensitive (610 nm) mechanism (Saunders, 1977).

Behavioural studies of cat photopic spectral sensitivity have produced an equally confusing picture. Bonaventure (1962) reported the cat's photopic spectral sensitivity to be the same as its scotopic spectral sensitivity; Gunter (1954) reported a two-peaked (560 and 460 nm) photopic function; LaMotte & Brown (1970) also reported a two-peaked photopic function but the peaks (523 and 564 nm) differed from those observed by Gunter. Of these cat psychophysical studies none used a common method and for procedural reasons were not ideal applications of the methods they did use. The difficulty for brightness matching with an animal (Gunter, 1954; Bonaventure, 1962) is that one needs to know already what the match is to consistently reinforce the animal only when it is correct. Gunter (1954) and Bonaventure (1962) 'solved' this dilemma by reinforcing their cats for whatever they did on trials which determined the match. LaMotte & Brown (1970) estimated cat photopic thresholds from the rod–cone break of dark-adaptation curves which is bumpy terrain even under more ideal conditions (Wooten & Butler, 1976), and influenced by differential rates of light and dark adaptation in the various mechanisms (Wooten, Fuld & Spillmann, 1975).

To this photopigment confusion has been added the suggestion that, under normal physiological conditions, the cat may restrict illumination of its retinae to mesopic levels through pupil constriction (LaMotte & Brown, 1970).

Considering the cat's prominence as a model of mammalian visual system function, it is unfortunate that such a fundamental aspect of its organization should remain so uncertain. In order to better our understanding of the cat's photopic mechanisms we have determined psychophysical spectral sensitivity using increment thresholds (ΔI), both large and small, and critical flicker frequency (c.f.f.) on a variety of white and chromatic backgrounds. We selected these test conditions because in humans (King-Smith & Carden, 1976) and other animals (Jacobs, 1981) these tests appear to produce the most discrepant results. Other procedures either produce similar results (e.g minimally distinct-border method yields results much like flicker methods) or results which appear to split the difference (e.g. direct comparison brightness matching) (Wagner & Boynton, 1972). Thus if the cat's photopic spectral sensitivity was dependent upon the spatio-temporal characteristics of the stimulus then increment thresholds and c.f.f. might likely reveal the difference. We selected a psychophysical approach for three reasons. First, we wished to examine wave-length sensitivity under normal physiological conditions to determine if a transition from rod to cone function was a natural occurrence in the cat or are the high light levels, achievable only with Maxwellian view or pupil dilation, necessary to consistently demonstrate certain cone functions, e.g. blue (LaMotte & Brown, 1970; Crocker *et al.* 1980). Secondly, we wished to avoid the sampling bias attendant to some micro-electrode recording techniques because if the influence of different cone mechanisms is unequally represented in different neurone types (Lennox, 1956), this factor could be the source of some of the variability in the physiological literature. Our third reason involves the hypothesis about why different psychophysical discriminations result in different spectral sensitivity outcomes. In particular King-Smith & Carden (1976) have suggested that in primates spectral increment thresholds for large- and long-duration increments are detected by wave-length opponent (e.g. colour) mechanisms while brief, flickering or small spectral increments are detected

by wave-length non-opponent (e.g. luminance) mechanisms. The cat seemed an interesting case in which to examine this hypothesis because it has so few wave-length opponent ganglion cells (4 %) compared to primates (64 %) (DeMonasterio & Gouras, 1975; Wienrich & Zrenner, 1983).

METHODS

Animals

Data were collected on a total of seven adult cats (six females, one male; all brown or grey tabbies). Three completed all testing while two additional cats participated in either large-increment threshold or c.f.f. studies. Each cat was maintained at 80 % of its free-food body weight with reinforcements obtained during testing, additional food in its home cage, daily vitamins and free access to water. The colony room was maintained on a 12 h light cycle. Prior to these experiments, each cat's thresholds for a white increment on a white background (Weber fraction) had been determined over a wide range of background luminance levels (Loop & Millican, 1983). Thus all of these cats were well trained in the procedures used here.

Apparatus

Our simultaneous two-choice testing apparatus was modelled after Berkley's (1970). It consisted of a testing box with a head chamber at one end into which the cat put its head. The head chamber contained two clear (90–92 % transmission from 400–640 nm) Plexiglas response keys through which the cat could view the stimulus screen and respond by pushing a key with its nose. Reinforcement (dilute canned cat food) was delivered just below and between the response keys. The testing box was housed in a larger light-tight box and faced the stimulus screen (Polocoat Glass-cat 3 M Co.) upon which stimuli and background were rear projected from outside the larger box. Unwanted illumination of the screen was eliminated by an arrangement of black cloth and cardboard so that only light from the slide projector lenses illuminated the viewing screen. The background extended over a large portion of the cat's field of view and was always on. The circular stimuli were projected upon the background with approximately square-wave onset. The luminance of the 2·3 cm stimulus at its edges was within 14 % of the luminance at the centre (Tektronix 1 deg luminance probe J6523). The wave-length and irradiance of the stimuli were controlled with interference filters (Corion) and neutral-density filters (Kodak No. 96). Utilizing a spectraradiometer (International Light IL 780), calibrated against a He–Ne laser, measurements on the cat's side of the viewing screen indicated that the half-band width of the light was no more than 12 nm and peak transmission was within 5 nm (usually 2 nm) of the filters stated value. The wave-lengths used were 399, 419, 438, 454, 480, 497, 518, 539, 561, 580, 599, 622 and 643 nm. Prior to psychophysical testing a given wave-length was always set at fixed-calibration irradiance value ($\mu W/Cm^2 . s$) which was measured with a digital radiometer (Tektronix J16, J6502 probe) flush against the viewing screen. The calibration irradiance varied among wave-lengths and was set by adjusting the bulb's voltage. This method is permissible because the bulb's output passed through an interference filter. During psychophysical testing the irradiance of the stimulus was adjusted downward from its calibration value with neutral-density filters.

The luminances of the backgrounds were also set at fixed calibration values. The white background and yellow background (Kodak filter no. 15) were set at 300 cd/m^2 and the magenta background (Kodak filter no. 30 plus 80A colour temperature correction filter) at 40 cd/m^2. The white background was used at several luminance levels which were achieved by reducing the calibration luminance with neutral-density filters (Corion, glass). The yellow background was reduced to 96 cd/m^2 with a neutral-density filter (0·5 log units) and the magenta background was used at its calibration luminance (40 cd/m^2). Background luminance calibrations were made with a digital photometer (Tektronix J16, probe J6503). The energy *vs.* wave-length distributions of a white (30 cd/m^2), the yellow and the magenta backgrounds are presented in Fig.1.

Large-increment thresholds and c.f.f. were determined with a response key to viewing screen distance of 6 cm and a stimulus size of 2.3 cm resulting in a maximum visual angle of 20 deg. However, because the cats appeared to make their decision about 4 cm from the key, stimulus size was probably around 13 deg. Small-increment thresholds were determined at a viewing distance

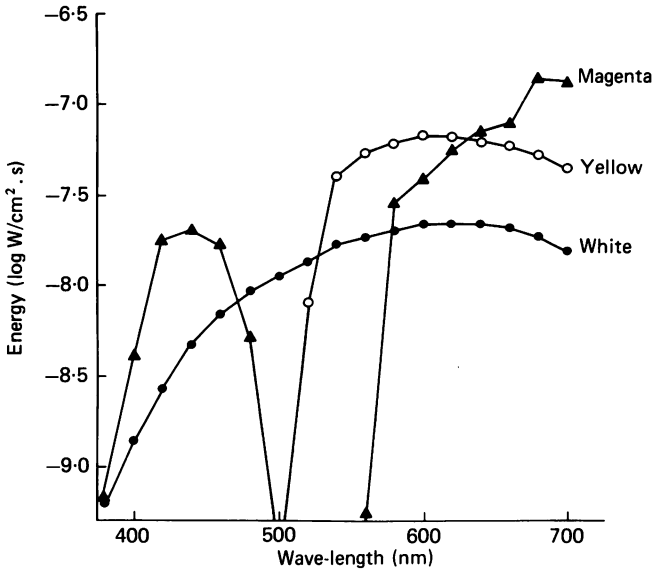

Fig. 1. Spectral energy distribution of white (30 cd/m²), yellow (96 cd/m²) and magenta (40 cd/m²) backgrounds.

of 40 cm for a stimulus size of 2 mm or 0·28 deg. At 6 cm the background was 94 × 74 deg while at 40 cm it was 32 × 10 deg. The width and height of the background are a different ratio because at 6 cm head-chamber size determined the background size.

The optical system which delivered the stimulus was different in each experiment. Large spectral increments were delivered from one slide projector which positioned the increment (right or left) by changing slides which were opaque except for a circular aperture. Interference filter and neutral-density filters were placed over the projector's lens. C.f.f. stimuli presented the cat with two equal intensity monochromatic stimuli (2·3 cm each) one of which flickered and one of which was steady. This was done by combining the output of two slide projectors at a large beam splitter. The flicker projector (lamp d.c. powered) had a variable speed sector disk in front of its lens so that approximately square-wave, 100% contrast, flicker was imparted to its projected image. The second projector imaged a steady spot of light upon the viewing screen in the opposite position (left or right) from where the flickering spot was projected. By placing an interference filter at the exit face of the beam splitter, and adjusting the intensity of the two projectors, we obtained two images on the viewing screen one flickering and one steady, of identical spectral composition and time average intensity.

For small spectral increments a one-channel projection system, that did not magnify the projected image of the aperture which controlled stimulus size, was used. This change, plus the use of a 500 W bulb, increased the available monochromatic stimulus irradiance by about 1·0 log unit and required that stimulus position be controlled by a moveable front-surface mirror.

The irradiance of the stimulus was measured for the 2·3 cm increment because the 2 mm increment did not fill the whole detecting surface of the irradiance probe, thus making calibration inaccurate. As both stimulus sizes were the result of changing the aperture in the optical system which was positioned in a collimated portion of the light path, irradiance (μW/cm²) was the same for both stimulus sizes.

Procedure

The response rules were the same during all testing. Correct responses were followed by reinforcement, a brief tone, and a 3 s intertrial interval. Incorrect responses were followed by no reinforcement and a 6 s intertrial interval. During an intertrial interval the stimulus was off, a white noise presented and responses reset the intertrial interval to 6 s. At the end of the intertrial

interval, a 1 s observation period began during which the stimulus and white noise were present but responses reset the period to 1 s. At the end of the observation period, the white noise terminated and the cat was free to make its choice. The left–right position of the correct stimulus was organized in a Gellerman series with a total sequence length of eighty. A correction procedure was used whereby four consecutive responses to one side held the correct stimulus on the opposite side until a correct response was made. Total trials, correct responses, responses to left and right key and number of responses made while the correction procedure was in force were recorded.

When observed, the cats appeared to look at the stimulus but we have no precise estimate of stimulus position in the cats' visual field during testing. The natural pupil was used and its area, according to the detailed study of Kappauf (1943), was 100 mm^2 at 0 cd/m^2, 85 mm^2 at 0·3 cd/m^2, 46 mm^2 at 3·0 cd/m^2, 15 mm^2 at 30 cd/m^2 and 6 mm^2 at 300 cd/m^2.

The cats were dark adapted for at least 30 min in a light-tight box before testing. They were transferred to the testing apparatus as quickly as possible with ambient light as low as possible. Our thinking was that the cats would quickly light adapt to the background and be at a steady level of adaptation by the time those trials which determined threshold were run; usually 10–15 min after testing began. The only exception to this procedure was testing on the 300 cd/m^2 white background; the cats were transferred directly from their carrying cages to the apparatus.

Thresholds were obtained through a method of limits procedure. Testing was conducted in forty trial blocks starting at a stimulus irradiance selected to be about 1·5 log units above threshold which always elicited at least 90 % correct responding. The stimulus was dimmed by 0·5 log units for every subsequent block of trials until a value was reached which elicited performance of 64 % correct or lower. A final block of trials was then conducted for a suprathreshold stimulus to determine if fatigue, satiation or any other non-stimulus variable could account for the decline in performance. From this daily frequency-of-seeing function the threshold was calculated to be that stimulus irradiance corresponding to 70 % correct. Appropriate compensation was made for the measured non-neutrality of the J6502 probe and neutral-density filters for wave-lengths shorter than 480 nm.

Two daily thresholds were determined for each wave-length for each cat. If the two thresholds differed by more than 0·5 log units, a third threshold was determined and averaged with the closest of the initial two thresholds. Grouped data were obtained by averaging the individual animal's average (log $\mu W/cm^2$) thresholds. The results of one animal were selected for individual presentation (triangles on each Figure if outside average data point). This cat was chosen because it participated in all experiments and generally showed the highest short wave-length sensitivity when 'blue' cones were involved. These irradiance thresholds were converted to quanta/cm^2.s. Spectral sensitivity functions were plotted in terms of the reciprocal of these photon thresholds. The sequence of wave-lengths tested was counterbalanced. The cats were tested 5 days each week. Explicit determination of the influence of the stimulus intensity at which testing was started (1·5–0·5 log units above threshold) indicated that it had no effect upon threshold. Repeated threshold determinations at a particular stimulus condition (561 nm increment on a 30 cd/m^2 white background) indicated that the cats' thresholds were stable across years.

In some sets of data the cats' sensitivity appeared to be determined by only one mechanism. In these cases the best-fitting visual pigment nomogram was determined by comparing the data with polynominal expressions of pigment nomograms provided by Dawis (1981). This was accomplished in an iterative fashion by varying the polynominal's λ_{max} in 1 nm steps and its vertical position in 0·05 log unit steps until the difference between the data and the polynominal's output was minimized. A computer spread-sheet program was used.

In preview the λ_{max} of the cats scotopic spectral sensitivity was best fitted by a 512 nm nomogram and photopic spectral sensitivity best fitted by linear combinations of 447 and 554 nm nomograms weighted to accommodate the animals' relative sensitivity at 454 and 561 nm. Where single nomograms are presented vertical position is the computational best fit; where combinations of nomograms are presented vertical positioning was by eye.

In the Figures which follow, we have not corrected our observed results for the influence of the cat's lens (Weale, 1954) or tapetum (Gunter, Harding & Stiles, 1951; Weale, 1953) because their effect is fairly small and their influence will generally be reflected in physiological and psychophysical studies. For some data, tapetum influence was calculated and compared to the best-fitting nomogram.

RESULTS

Large-increment-threshold spectral sensitivity

Because there is general agreement on the cat's absolute dark-adapted (scotopic) spectral sensitivity, we felt a redetermination would constitute a meaningful validation of our methods. Fig. 2 illustrates the mean sensitivity of the cats against a dark

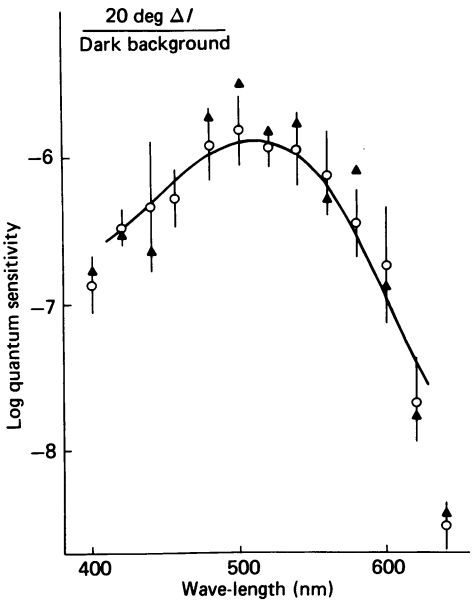

Fig. 2. Increment-threshold sensitivity on a dark background for a 20 deg stimulus. Continuous curve is a 512 nm nomogram. In this and all subsequent Figures, circles and bars represent group mean ± one standard deviation; triangles represent one cat's data.

background. Best sensitivity was observed at 497 nm and the best-fitting nomogram had a λ_{max} of 512 nm. These wave-lengths are near previous behavioural (Gunter, 1952; LaMotte & Brown, 1970) and physiological estimates (Daw & Pearlman, 1970; Andrews & Hammond, 1970). Application of the 'yellow' tapetal correction (Weale, 1953) to the observed sensitivity resulted in a best-fitting nomogram whose λ_{max} was 503 nm, a value quite close to spectroscopic (502 nm) results for extracted visual purple (Lythgoe, 1937).

Fig. 3 illustrates the cat's mean spectral sensitivity on white backgrounds of 0·3, 3, 30 and 300 cd/m^2. The cats were most sensitive to 497 nm on 0·3 and 3 cd/m^2 white backgrounds suggesting that rods were most sensitive under these conditions. When the luminance of the white background was increased to 30 cd/m^2 the cats were most (and approximately) equally sensitive to 561 and 454 nm and showed a relative reduction in sensitivity at 497 nm. At a background luminance of 300 cd/m^2 the cats also evidenced sensitivity peaks at 561 and 454 nm but the 454 nm peak was relatively higher. These results suggested that spectral increments on a white background of 30 cd/m^2, or brighter, were detected by cones. At the same time these results suggested two things at odds with some of the physiological data. First, if

'blue' cone influence was as rare as is usually suggested, why were the cats so sensitive to short wave-lengths? Secondly, if cats possess a 500 nm photopic mechanism, why were they relatively insensitive to this wave-length at photopic levels? Both of these questions were approached with the use of chromatic backgrounds.

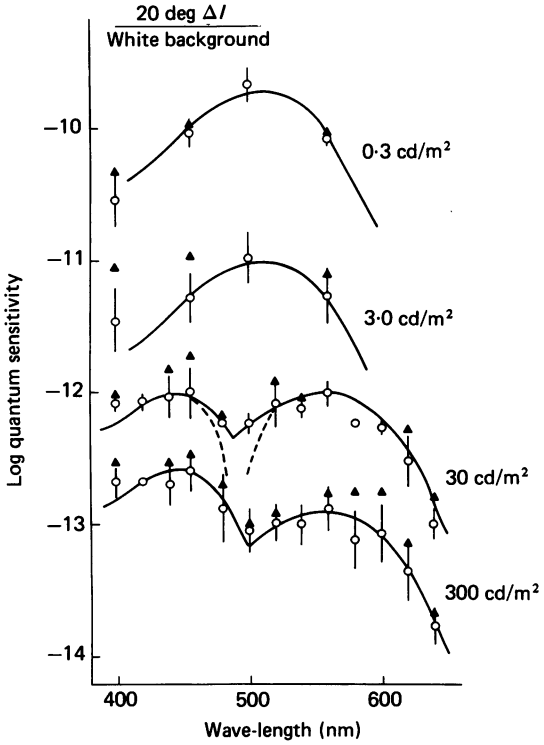

Fig. 3. Increment-threshold sensitivity on white backgrounds (0·3, 3·0, 30 and 300 cd/m²) for a 20 deg stimulus. Continuous curve for 0·3 and 3·0 cd/m² background is a 512 nm nomogram. Continuous curves for 30 and 300 cd/m² backgrounds represent the more sensitive of 447 and 554 nm nomograms weighted equally (30 cd/m²) or 1·23 to 1 (300 cd/m²). Dashed curve (30 cd/m²) represents the linear subtraction of 447 and 554 nm nomogram sensitivities equally weighted.

One possible explanation of the cat's high sensitivity to short wave-lengths was that the β peak of the long-wave-length cone was responsible for detecting the stimulus. A second possibility was intraocular-instigated fluorescence detectable by the long-wave-length cone. In either case, or their combination, sensitivity to short wave-lengths should decline in tandem with long-wave-length sensitivity if it was suppressed by a yellow background. At the same time we had to select a yellow background which was photopic for the cat, i.e. equivalent to at least 30 cd/m² of white light. In this regard our luminance (human) measuring instruments were unsuitable. We therefore selected a yellow background which produced the same threshold at 454 nm as did the 30 cd/m² white background making the yellow background photopic, by definition, at least for short wave-lengths. This value, 96 cd/m² (Fig. 1), was ascertained by several threshold determinations on one cat.

As was our design, Fig. 4*A* illustrates that on this yellow background the cat's sensitivity was the same at 454 nm as it had been on the 30 cd/m² white background. However, their long-wave-length sensitivity was reduced by about 0·45 log units in keeping with a selective reduction in the sensitivity of their long-wave-length cone. This result indicates that the cat's short- and long-wave-length sensitivity is not mediated by a single photopigment. The continuous curve represents the best-fitting nomogram for the wave-lengths from 399 to 487 nm and has a λ_{max} of 447 nm.

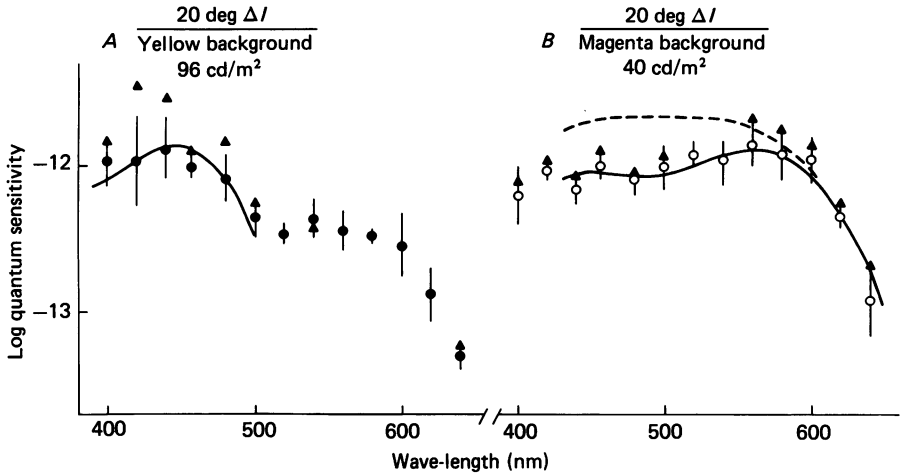

Fig. 4. *A*, increment-threshold sensitivity on a yellow background for a 20 deg stimulus. Continuous curve represents 447 nm nomogram. *B*, increment-threshold sensitivity on a magenta background for a 20 deg stimulus. Continuous curve represents the additive sensitivity of 447 and 554 nm nomograms weighted 1 to 2·05. Dashed curve represents the additive sensitivity of 447, 512 and 554 nm nomograms equally weighted.

Physiological studies reporting a 500 nm photopic process in cats have generally used chromatic (e.g magenta) backgrounds to exclude rod contribution and depress the sensitivity of the short- and long-wave-length cones (Crocker *et al.* 1980; Schuurmans, 1981). We took a similar approach selecting a blue-accentuated magenta background (Fig. 1) producing increment thresholds at 454 and 561 nm that were nearly the same as were obtained on the 30 cd/m² white background. The cats' sensitivity at 500 nm on a magenta background (Fig. 4) is somewhat higher than on an equivalent white background but was still less than that observed at 454 and 561 nm. The continuous curve fitted to these data represents the additive combination of 447 and 554 nm nomograms in a ratio of 1 to 2·05. The dashed curve represents the additive combination of 447, 512 and 554 nomograms weighted equally.

C.f.f. spectral sensitivity

With humans and other primates c.f.f. photopic spectral sensitivity is generally obtained by using a criterion frequency believed to exceed the temporal resolution of primate rods (e.g. 25 Hz). This belief is questionable for primates (Conner & MacLeod, 1977) and wrong for the cat whose rods can support psychophysical c.f.f. at frequencies up to 35–45 Hz (Kappauf, 1937; Loop, Petuchowski & Smith, 1980).

Consequently, to ensure cone mediation on the basis of frequency alone we needed to use a temporal resolution of at least 50 Hz. Unfortunately the intensity of monochromatic light available to us was not sufficient. In order to test a wide range of wave-lengths we first used a c.f.f of 10 Hz; a frequency slightly on the fast side of the peak of the cat's temporal-contrast sensitivity function (Loop & Berkley, 1975; Blake & Camisa, 1977) and a frequency used before in the determination of animal photopic spectral sensitivity (Polson, 1968). We then increased the frequency to 20 Hz and determined a second function between 454 and 643 nm (the cats were unable to resolve this frequency below 454 nm). At both frequencies rod contribution was eliminated by testing upon a 30 cd/m^2 white background (see Fig. 3 and Daw & Pearlman, 1969; Enroth-Cugell, Hertz & Lennie, 1977).

Psychophysical testing and threshold determination were conducted as in the increment threshold experiment the only difference being that now the cats had to distinguish the flickering stimulus from the steady one.

Fig. 5 presents the cats' c.f.f. spectral sensitivity on a 30 cd/m^2 white background. At 10 Hz three points are clear. First, the curve indicates better absolute sensitivity over most of the spectrum than the increment-threshold curve, a finding compatible with the fact that cats are more sensitive to intermediate temporal frequencies (10 Hz) than to zero temporal frequency (the increment threshold condition) (Blake & Camisa, 1977). Secondly, the 10 Hz curve peaks at 561 nm suggesting that the function is photopic. Thirdly, sensitivity is markedly reduced at short wave-lengths compared to the peak around 561 nm and is best fitted by a 554 nm nomogram. Correction of the 10 Hz data for the influence of a 'yellow' tapetum (Weale, 1953) resulted in a best-fitting nomogram of λ_{max} 552 nm.

The results obtained at 20 Hz, which are displaced downward by 1·0 log unit from their true position, indicate reduced sensitivity relative to 10 Hz, as the cat's temporal-contrast sensitivity would predict. However the spectral sensitivity function is now fairly flat from 454 to 580 nm. The continuous curve fitted to these data is the same linear addition of 447 and 554 nomograms as used for the magenta background data (Fig. 4).

Small-increment-threshold spectral sensitivity

Three cats, all of which participated in the large-increment-threshold and c.f.f. experiments, were studied. Testing began by gradually increasing viewing distance from 6 to 40 cm, with the physical size of the stimulus increment held constant at 2·3 cm. At 40 cm, increment thresholds were then determined for 454, 497 and 561 nm (30 cd/m^2 white background) to establish if the change in viewing distance and concomitant reduction in stimulus size (to 3·3 deg) and background size (to 32 × 10 deg) influenced the cat's sensitivity.

Following this the stimulus size was reduced from 3·3 to 0·28 deg by replacing the 2·3 cm optical system aperture with a 2 mm aperture. The cat's acuity being about five times worse than a human's (Berkley, 1976) we selected a 0·28 deg increment because this increment size is five times larger than what constitutes a 'small' stimulus size for humans (King-Smith & Carden, 1976; Finkelstein & Hood, 1982).

The cat's sensitivity for the 2·3 cm increment, now 3·3 deg at a viewing distance of 40 cm, on a 30 cd/m^2 background remained unchanged, in both shape and absolute

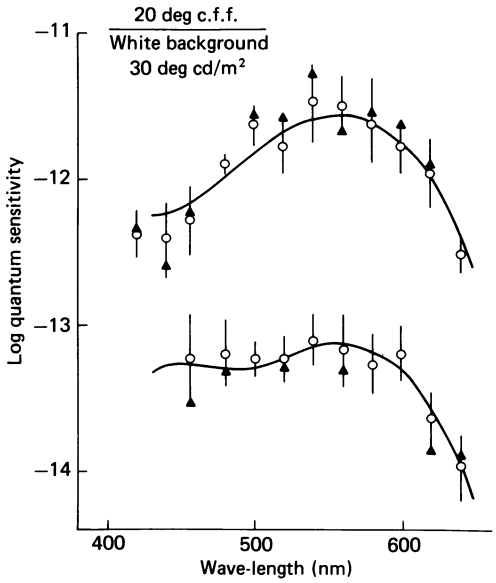

Fig. 5. Critical flicker frequency for 10 Hz (upper circles) and 20 Hz (lower circles) on a 30 cd/m² white background. The 10 Hz continuous curve is a 554 nm nomogram. The 20 Hz continuous curve is a linear addition of 447 and 554 nm nomograms in a ratio of 1 to 2·05. The 20 Hz data is displaced by one log unit below its true position.

sensitivity, for 561, 497 and 454 nm. This indicated that the move back to 40 cm and the attended changes in stimulus and background size did not exert any generalized effect upon the cats' sensitivity.

Fig. 6 (upper curve) presents the cats' increment-threshold spectral sensitivity on a 30 cd/m² white background when the increment subtended 0·28 deg. The best-fitting nomogram, when all the data were included, had a λ_{max} of 558 nm but was clearly spuriously low of the cats' sensitivity from 497 to 643 nm. Between 497 and 643 nm this function is best fitted by a nomogram whose λ_{max} is 554 nm and reflects an over-all sensitivity reduction of about 1·0 log units, relative to sensitivity when the increment was 20 deg. Also there is no indication of a contribution by any mechanism other than the 'green' cone. In this regard the shape of small-increment-threshold function greatly resembles the 10 Hz c.f.f function (Fig. 5) but here the absolute sensitivity difference is about 2·0 log units. The precipitous decline in sensitivity for wave-lengths shorter than 497 nm is probably the result of chromatic aberration introduced by the cat's lens. The apparent lack of any 'blue' cone influences on the cats' sensitivity to the small increment, afforded another opportunity to determine if any contribution from a 500 nm photopic mechanism could be demonstrated. We proceeded by determining increment threshold for several wave-lengths on a bright (96 cd/m²) orange (Kodak no. 21 filter, cut-off 540 nm) background. As Fig. 6 (lower curve) illustrates, the cats' sensitivity still reflected only the activity of the long-wave-length mechanism.

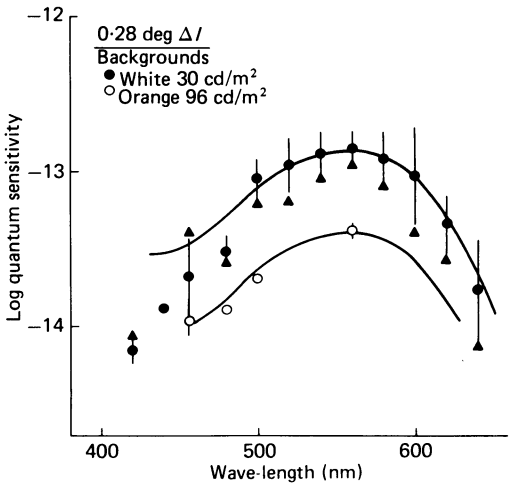

Fig. 6. Increment-threshold sensitivity for a 0·28 deg stimulus on a 30 cd/m² white background (filled circles) and a 96 cd/m² orange background (open circles). Both continuous curves are a 554 nm nomogram.

DISCUSSION

Large-increment-threshold spectral sensitivity

These data, e.g. Figs. 2 and 3, paint a fairly clear picture of the luminance boundaries of rod and cone vision in the cat. When the background luminance is 3·0 cd/m², or lower, the cat's sensitivity appears to be determined by a single mechanism most sensitive around 500 nm, i.e. rods. When luminance is 30 cd/m², or higher, the cat's sensitivity appears to be determined by at least two photoreceptors with λ_{max} values around 447 and 554 nm, i.e. cones. The centre of the mesopic zone, if defined as equal sensitivity at 454, 497 and 561 nm, lies at about 10 cd/m² of white light. This value is quite close to previous behavioural estimates of the cats' mesopic zone (natural pupil) based upon the effect of luminance upon critical flicker fusion (Kappauf, 1937; Loop *et al.* 1980) and acuity (Pasternak & Merigan, 1981).

This pronounced influence of ambient illumination upon the cat's spectral sensitivity explains much of the variation in behavioural results of Gunter (1954) and Bonaventure (1962). Following 30 min of light adaptation, sometimes sunlight, Gunter's cats were tested in the presence of considerable illumination (six 100 W light bulbs along the runway and a 300 W bulb over the start box). The spectral sensitivity function he determined is similar to our results on a 30 cd/m² white background. Bonaventure (1962), on the other hand, tested her cats in an ambient illumination of only 3 lx and the resultant function resembles our results on equivalent and dimmer backgrounds.

It is noteworthy that the cat's sensitivity was unaffected by changing the viewing distance to 40 cm; this suggests that the results of Figs. 2, 3 and 4 apply to stimulus sizes down to 3·3 deg.

The increment-threshold functions obtained with large stimuli support the most

commonly reported physiological findings for the cat, namely the existence of 'blue' and 'green' cones. Furthermore, they lend credence to physiological reports that 'blue' cones are not feeble in their influence (Crocker *et al.* 1980; Schuurmans, 1981). At the same time these increment-threshold data argue against a 500 nm process active at photopic levels because, even under chromatic adaptation, sensitivity shows a drop in this region of the spectrum.

The correct interpretation of this mid-spectrum sensitivity dip is bounded by the two simplest ways in which a 'blue' and 'green' mechanism might combine their influences; namely linear addition or subtraction of their sensitivities; both outcomes have been reported in neurophysiological data. Zrenner & Gouras (1979) found that the spectral sensivitity of both the negative-on and negative-off electroretinogram (e.r.g.) responses are closely approximated by an additive combination of two cones nomograms (λ_{max} 450 and 555 nm) while spectral sensitivity based upon the positive-on e.r.g. response agreed with a subtraction interaction. Pearlman & Daw (1970) found a similar subtractive interaction in the behaviour of chromatically opponent neurones in the cat's lateral geniculate nucleus. With large increments the cat's psychophysical photopic spectral sensitivity has a mid-spectrum dip around 500 nm. On white backgrounds (Fig. 3, 30 and 300 cd/m^2) the cat's sensitivity is close to that expected from detection based upon the most sensitive mechanism acting independently (continuous curves Fig. 3). A subtractive interaction predicts lower than observed mid-spectrum sensitivity (dashed curve Fig. 3) while an additive interaction predicts higher mid-spectrum sensitivity (continuous curve Fig. 4*B*). Sensitivity on a magenta background (Fig. 4*B*) is well predicted by the additive combination of 447 and 554 nm nomograms (continuous curve). The dashed curve illustrates what would be expected from the additive combination of 447, 512 and 554 nm nomograms. Its vertical position has been set to match the cat's sensitivity at the longest wave-lengths tested. These results suggest no contribution from a 500 nm mechanism active at 30 cd/m^2 or brighter. Likewise the report of a long-wave-length mechanism (Saunders, 1977) is not supported by these data.

C.f.f. spectral sensitivity

In trichromatic mammals photopic spectral sensitivity based upon c.f.f. shows no contribution from 'blue' cones and an additive contribution from the two long-wave-length cones (Jacobs, 1963; DeValois, Morgan, Polson, Mead & Hall, 1974; Boynton, 1979). In dichromatic mammals only the influence of the one long-wave-length cone is observed (Polson, 1968). For a c.f.f. of 10 Hz (Fig. 5 upper curve) the cat's sensitivity is well described by a 554 nm mechanism acting alone. This result is similar to the behavioural results obtained by LaMotte & Brown (1970) whose psychophysical task was detection of a flickering light (8 Hz) following intense-light adaptation. They, like we, found the cat to be much more sensitive around 560 nm than at shorter wave-lengths.

The results obtained at 20 Hz (Fig. 5 lower curve) are best accounted for by an additive contribution from both 'blue' and 'green' cones. This result is surprising in light of the results at 10 Hz. However, a very similar result was obtained in conjunction with a previous analysis of cat c.f.f. where an abbreviated spectral sensitivity function was obtained for 35 Hz (Loop *et al.* 1980), which indicated essentially equal sensitivity at 454, 497 and 561 nm.

The typical absence of 'blue' cone influence on c.f.f. is generally attributed to their intrinsic poor temporal response combined with a lack of input to the ganglion cells with the best temporal resolution (Boynton, 1979). Neither of these primate characteristics may be true for the cat. Thus 'blue' cones have been shown to mediate the e.r.g. at a frequency of 40 Hz (Rabin, Mehaffey & Benson, 1976) and also influence brisk-transient ganglion cells (Crocker *et al.* 1980), and Y cells (Rodieck & Dineen, 1985). Both of these facts are compatible with the results at 20 Hz (Fig. 5) and 35 Hz (Loop *et al.* 1980). What is unclear is why the 'blue' cones should be so uninfluential at a frequency of 10 Hz.

Small-increment-threshold spectral sensitivity

The cat's spectral sensitivity function for small (0·28 deg) increments is very similar to its 10 Hz c.f.f. spectral sensitivity function albeit displaced 100-fold. The reduction in absolute sensitivity, that follows the reduction in stimulus size, and the loss of a 'blue' cone contribution, parallel the psychophysical results obtained in humans (King-Smith & Carden, 1976; Finkelstein & Hood, 1982). To our knowledge no similar data are available from any other non-humans.

Determinants of cat photopic spectral sensitivity

The cat's photopic wave-length sensitivity is that of a dichromat. At long wave-lengths they are most sensitive to greenish yellow light and our two estimates of this mechanism's λ_{max}, both 554 nm, are very close to all previous estimates of the maximum sensitivity of cats' most common cone. Our estimate of their short-wave-length mechanism's λ_{max}, at 447 nm is somewhat shorter than other reports, 460 nm being the longest (Schuurmans, 1981) and is not as secure because no stimulus conditions isolated its response completely from the 'green' cones influence.

We find no evidence for a 500 nm process active at photopic levels. Previous claims have been based upon physiological data showing sensitivity shifts during dark adaptation that resemble a rod–cone break (Ringo *et al.* 1977; Crocker *et al.* 1980) or sudden changes in temporal resolution (Schuurmans, 1981) as illumination is increased with spectral sensitivity remaining unchanged and rod-like in both cases. Two points are worth noting. First, breaks in the temporal resolution function that depend solely on rods have been reported physiologically (Green & Siegel, 1975) and psychophysically (Conner & MacLeod, 1977). Secondly, cat rods have two retinal pathways through which they may influence ganglion cells: one direct and one via the cone pathway (Sterling, 1983). It seems possible that a shift from one pathway to the other, as dark adaptation proceeds, might mimic a rod–cone-like sensitivity change at the ganglion cell level. Very recently two electrophysiological studies have implicitly (Rodieck & Dineen, 1985) and explicitly (Jacobs & Neitz, 1986) concluded that the cat has no middle-wave-length mechanism active at photopic levels.

We also find no support for the assertion (LaMotte & Brown, 1970) or suggestion (Crocker *et al.* 1980) that extraordinary light levels are required to elicit cone-mediated vision in cats. Our results reject the notion that cats normally run around with their retinae in perpetual twilight (LaMotte & Brown, 1970). By all psychophysical criteria when ambient luminance is above 10 cd/m^2 the vision of cats is based upon cones.

It is becoming clear that photopic spectral sensitivity functions based upon increment thresholds for large stimuli of long duration are multipeaked in man (Sperling & Harwerth, 1971) and every other vertebrate that is at least a dichromat (Jacobs, 1981). These peaks, or rather the valleys which define them, are probably the result of inhibitory interactions between the cones involved and hence reflect the activity of wave-length-opponent neurones. Single-peaked photopic spectral sensitivity function, the typical result if significant temporal or spatial resolution is required, are viewed as additive interactions between the cones involved and hence reflect the activity of non-opponent neurones (King-Smith & Carden, 1976).

The cat appears to fit this general scheme fairly well even to the point of showing a conspicuous notch in its large-increment-threshold spectral sensitivity on photopic white backgrounds (Fig. 3). In species where the increment-threshold notch is surely the result of opponent interactions between cones (Sperling & Harwerth, 1971; King-Smith & Carden, 1976), its depth is never what strict subtraction would predict (i.e. no wave-lengths are invisible) and is influenced by the chromatic content of the background and the temporal and spatial frequency content of the increment (Thornton & Pugh, 1983). Thus the significant point may be that the cat's mid-spectrum sensitivity falls well below what the additive sensitivity of its two cones would predict and is sometimes observed (Figs. 4*B* and 5, 20 Hz). Also if our estimate of the 'blue' mechanism's λ_{max} is in error it is likely too short. If this be the case then the cat's sensitivity to large increments at 480 and 497 nm falls below independence and toward subtraction.

Significant temporal (Fig. 5, 10 Hz) or spatial (Fig. 6) resolution is mediated by only the long-wave-length cone or by an additive contribution of the long- and short-wave-length cones (Fig. 5, 20 Hz). This latter observation differs greatly from observations made on other mammals where 'blue' cone influence is almost exclusively confined to opponent mechanisms. It is now clear, however, on the basis of e.r.g. (Zrenner & Gouras, 1979), ganglion cell recording (Crocker *et al.* 1980) and psychophysical c.f.f. (Fig. 5; Loop *et al.* 1980) that, in cats, 'blue' cones influence non-opponent mechanisms. This situation may explain some of the cat's problem with colour discrimination. It has been proposed that the extent to which different parts of the spectrum are coloured, i.e. saturation, is dependent upon the relative activity of wave-length-opponent and non-opponent neurones (DeValois, Abramov & Jacobs, 1966). This hypothesis explains why, in trichromatic primates, short wave-lengths are so potentially chromatic and middle wave-lengths, especially 560 nm, are not. The 'blue' cones influence opponent neurones almost exclusively. The cat enjoys no part of the spectrum free from good non-opponent mechanism sensitivity and hence all colours, by primate standards, may be desaturated.

The fact that so many different species have more than one photopic spectral sensitivity function, the cat having three on a 30 cd/m^2 background, raises a significant procedural dilemma for any visual experiment designed to use different, but equally stimulating (bright), wave-lengths. Upon which spectral sensitivity outcome should equal brightness be based? The question is not rhetorical but it would seem advisable to derive spectral sensitivity in a way which closely approximates the stimulus situation of any subsequent visual experiment which relies upon different wave-lengths of equal brightness. It might be a mistake, for example, to

test two-choice wave-length discrimination of two steady stimuli with brightness matched on the basis of the cat's c.f.f. photopic spectral sensitivity.

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