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CAT COLOUR VISION: ONE CONE PROCESS OR SEVERAL?

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SUMMARY

1. Peripheral mechanisms that might contribute to colour vision in the cat have been investigated by recording from single units in the lateral geniculate and optic tract. Evidence is presented that the input to these cells comes from a single class of cones with a single spectral sensitivity.

2. In cats with pupils dilated a background level of 10–30 cd/m^2 was sufficient to saturate the rod system for all units. When the rods were saturated, the spectral sensitivity of all units peaked at 556 nm; this was true both for centre and periphery of the receptive field. The spectral sensitivity curve was slightly narrower than the Dartnall nomogram. It could not be shifted by chromatic adaptation with red, green, blue or yellow backgrounds.

3. In the mesopic range (0·1–10 cd/m^2), the threshold could be predicted in terms of two mechanisms, a cone mechanism with spectral sensitivity peaking at 556 nm, and a rod mechanism with spectral sensitivity at 500 nm. The mechanisms were separated and their increment threshold curves measured by testing with one colour against a background of another colour. All units had input from both rods and cones. The changeover from rods to cones occurred at the same level of adaptation in both centre and periphery of the receptive field. Threshold for the cones was between 0·04 and 0·25 cd/m^2 with the pupil dilated, for a spot covering the centre of the receptive field.

4. None of the results was found to vary between lateral geniculate and optic tract, with layer in the lateral geniculate, or with distance from area centralis in the visual field.

5. The lack of evidence for more than one cone type suggests that colour discrimination in the cat may be a phenomenon of mesopic vision, based on differences in spectral sensitivity of the rods and a single class of cones.

INTRODUCTION

There is little doubt that cats have some degree of colour vision. When brightness and other cues are carefully eliminated cats can be trained to distinguish between red and green lights (Sechzer & Brown, 1964; Meyer & Anderson, 1965) and also between red and blue lights or red and yellow lights (Mello & Peterson, 1964). Previous failures to train cats to discriminate colour (Meyer, Miles & Ratoosh, 1954; Gunter, 1954*b*; DeVoss & Ganson, 1915) have been explained by methodological difficulties or by lack of persistence on the part of the investigator.

To make a discrimination between one wave-length and another, an animal must have at least two types of receptors with different spectral sensitivities. The receptors may be two types of cones, or they may be rods and one type of cone (McCann & Benton, 1968). Some animals even have two types of rods, e.g. the frog (Walls, 1942), but this is unusual. At present it is not known whether the cat has more than one type of cone, and makes wave-length discrimination on this basis, or whether it makes wave-length discriminations using the rods in conjunction with a single type of cone.

Several investigations have shown that cats have at least one cone process, with a different spectral sensitivity from that of the rods. The scotopic spectral sensitivity peaks at about 500 nm, whereas the photopic spectral sensitivity peaks at about 556 nm (Granit, 1943; Weale, 1953*b*, 1957; Dodt & Walther, 1958*a*, *b*) and this Purkinje shift has been confirmed by others (Gunter, 1952, 1954*a*; Dodt & Enroth, 1953; Barlow, Fitzhugh & Kuffler, 1957*a*; Dodt & Elenius, 1960). No investigation has conclusively demonstrated the existence of more than one cone process. The work of Granit (1943, 1945, 1947) suggests three cone processes, but his modulator curves were obtained by subtracting the visual purple curve from the actual measurements of spectral sensitivity. This procedure can lead to spectral sensitivities peaking at several different wave-lengths when there are only two basic processes involved. Other results, such as the variation in the time course of the spike train of ganglion cells with wave-length (Donner, 1950) and the variation of latency with wave-length (Lennox, 1956; Ingvar, 1959) can be explained as well by a single cone process interacting with the rods, as by several cone processes. Such mesopic interactions can also account for the two humps seen in some spectral response curves (Suzuki, Taira & Motokawa, 1960; Okuda, Taira & Motokawa, 1962). None of these experiments have determined the range over which both rods and cones are active, or attempted to eliminate the rods. This paper describes the manner by which the rods and cones together determine thresholds in the mesopic range, and the level

at which the rods saturate. By saturating the rods, it is possible to study the cones in isolation, and seek evidence for or against the existence of more than one cone process.

METHODS

Eleven mature cats weighing 2·0–3·5 kg were anaesthetized with a mixture of halothane, nitrous oxide and oxygen. Following cannulation of the trachea and femoral vein the animal was placed in a stereotaxic head holder which did not obstruct the visual fields. A small hole was made in the cranium and dura, and then sealed off with dental impression compound after introduction of the micro-electrode. Complete paralysis of eye movements necessitated a continuous infusion of gallamine triethiodide (5 mg/kg.hr) and *d*-tubocurarine (1 mg/kg.hr) (Rodieck, Pettigrew, Bishop & Nikara, 1967). A constant volume pump (Harvard Apparatus Co.) ventilated the animal with warm humidified air. When all surgical procedures were complete, halothane was stopped, and light anaesthesia maintained with either 70 % nitrous oxide and 30 % oxygen, or intraperitoneal Pentothal (20–30 mg initially and 10 mg/hr thereafter). Electroencephalographic monitoring showed high voltage 2–5/sec slow waves indicative of sleep in all animals. The electrocardiogram and rectal temperatures were also recorded, and body temperature maintained with a heating pad (Gorman–Rupp). Dilatation of the pupils and paralysis of accommodation were achieved with atropine, and the eyes were refracted with a retinoscope and focused on a tangent screen with the appropriate contact lenses. An ophthalmoscope and corner cube were used to plot the position of the area centralis on the screen. Each experiment lasted from 18 to 36 hr and the preparation remained stable throughout. One or more electrolytic lesions were made during each electrode penetration. At the end of the experiment the animal was perfused with formol saline, and all electrode placements were subsequently confirmed histologically.

Extracellular recordings were made from single cells with a tungsten micro-electrode (Hubel, 1957), coupled through a field effect transistor source follower to a pre-amplifier with cut-offs at 140 Hz and 5 kHz, and then to a Tektronix RM 565 oscilloscope and audio monitor. Amplified spikes also passed through a window with adjustable upper and lower limits, and were displayed as a series of dots on a Tektronix RM 564 storage oscilloscope (Wall, 1959). The source follower, pre-amplifier, window and spot plotter were designed and built by Mr D. C. Freeman.

Receptive fields were found and plotted on a tangent screen placed about 57 in. from the cat. They were all of the centre-surround type described by Kuffler (1953). The size of the centre of the receptive field was determined by observing the response to small spots of light and/or measuring the thresholds for a series of spots of different areas centred on the receptive field (Barlow, 1953). The two methods gave approximately the same centre size. Thresholds were determined approximately by listening to the loudspeaker, then more exactly by observing the response to several intensities around this value on the storage oscilloscope, three records being made at each intensity.

Monochromatic light was produced by a Leitz Prado 500 projector, with Baird Atomic Type B-1 interference filters (half-width about 7 nm) placed in front of the objective. The interference filters covered the range 420–640 nm in 10 nm steps, and 400–420 nm and 640–700 nm in 20 nm steps. The quantum flux produced by projector plus one interference filter, compared to the quantum flux produced by projector plus another interference filter was measured with a thermopile (Kipp & Zoner, Delft, Holland, model E-20), and the results are given by the lower set of points in Fig. 1. The spectral distribution of the white light emitted by the projector was calculated from these points and the transmissions of the interference filters. The latter were measured in a Cary 14 spectrophotometer (Applied Physics Corp.), with appropriate corrections for the fact that the light was not collimated. The results of these calculations for the spectral distribution at a surface of luminance 1500

cd/m² are given by the upper set of points in Fig. 1, the curve being drawn by hand through them. The units on the vertical axis were determined from the relationship: 680 lumens of white light is equivalent to 1 W of 556 nm for human photopic vision (Pirenne, 1961*a*).

The effectiveness of one wave-length compared to another, for a particular visual pigment or process, can be determined from the action spectrum of the process involved. The effectiveness of white light can be determined by multiplying the action spectrum of the process by the spectral distribution of the projector at each wave-length, then integrating under the resultant curve. These calculations have been made for the spectral curves for cat photopic and scotopic vision, and are given in the Table of equivalences (Table 1).

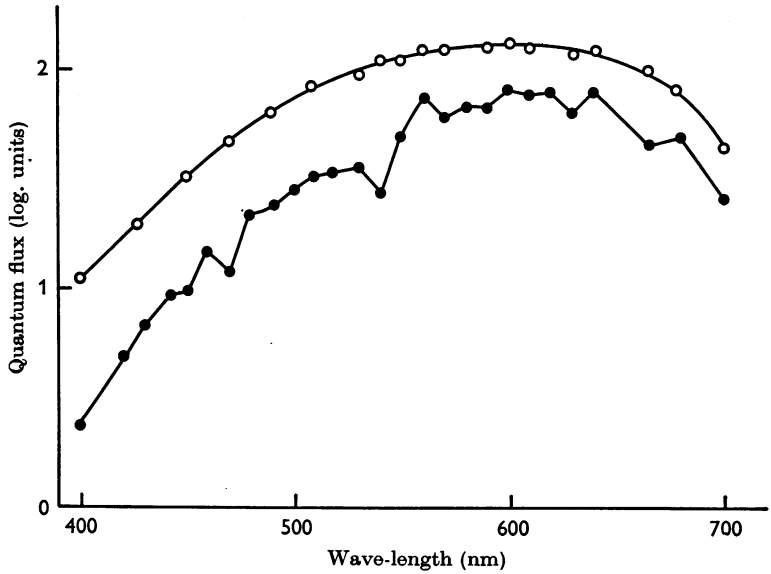

Fig. 1. Spectral distribution of the projector, when illuminating a white card to give luminance 1500 cd/m². Upper curve gives the quantum flux in the plane of the card per 10 nm of wave-length. Lower points give the quantum flux in the plane of the card with the interference filters interposed. A quantum flux of $1{\cdot}28 \times 10^{12}$ quanta $cm^{-2}\ sec^{-1}$ is zero on the log. scale.

TABLE 1. Amounts of monochromatic light which will have the same effect as a white light of luminance 1 cd/m² with the spectral distribution of the projector used:

Wave-length	Quantum flux (quanta $cm^{-2}\ sec^{-1}$)	log. quantum flux ($1{\cdot}28 \times 10^{12}$ quanta $cm^{-2}\ sec^{-1}$ = 0)
A For cat scotopic vision (visual pigment peaking at 500 nm)		
556	$8{\cdot}8 \times 10^{11}$	−0·16
590	$5{\cdot}1 \times 10^{12}$	0·60
480	$3{\cdot}44 \times 10^{11}$	−0·57
500	$3{\cdot}2 \times 10^{11}$	−0·60
B For cat photopic vision (curve of Fig. 10 peaking at 556 nm)		
556	$1{\cdot}28 \times 10^{12}$	0
590	$1{\cdot}68 \times 10^{12}$	0·12
480	$2{\cdot}8 \times 10^{12}$	0·34

The intensity of the stimulus in this paper is usually expressed in terms of cd/m² at the screen, because this is the only accurate measurement that can be made. The cat is looking at this with a dilated pupil. In order to get an approximate idea of what the brightness would have to be if the cat had a normal pupil, the values must be multiplied by 10. In order to express the results in terms of retinal illumination, the values must be multiplied by 200, to be converted into trolands. The latter factor is also approximate, and assumes (i) that the cat dilated pupil is 100 mm², and (ii) that man's retinal image is 1·37 as wide as that of the cat (Walls, 1942), so that the correct definition of a cat troland, for comparison with man, is the retinal illumination when 1 cd/m² is seen through a pupil area of 0·5 mm².

RESULTS

PART I. MESOPIC VISION

The first part of the paper analyses the cat's mesopic vision, where both rods and cones are active. Four questions were asked: (i) do the rods saturate? (ii) does the level of rod saturation vary from unit to unit? (iii) what is the extent of mesopic vision, i.e. where is cone threshold in relation to rod saturation? (iv) can the thresholds in the mesopic range be explained simply in terms of two processes, one cone, and one rod?

The questions were answered by a limited application of the Stiles two-colour increment threshold technique (Stiles, 1949, 1959). This involves measuring the threshold for a spot of one wave-length against a background of another wave-length, for various intensities of background. In order to bring out the rods, one uses a test spot that is particularly effective for them, and a background that is particularly effective in adapting the cones. In order to bring out the cones, the wave-lengths of spot and background are interchanged. To prove that the particular increment threshold curve obtained belongs to the rods, or the cones, some measure of the spectral sensitivity is obtained by varying the wave-length of the spot, the wave-length of the background, or both. We chose 480 nm as a wave-length likely to stimulate the rods rather than the cones, and 590 nm as a wave-length likely to stimulate the cones rather than the rods. Other wave-lengths might give more separation between rods and cones, but would not be as efficient, because of the fall off in sensitivity of the two processes, and of the emission of the projector, at both ends of the spectrum.

Figures 2–5 describe a series of these increment threshold measurements, all performed on the same unit. The size of the test spot and background, the timing and the procedure for determining threshold were kept constant throughout the series of measurements, so that one measurement could be compared with another. The spot was $1\frac{1}{2}°$ in diameter, centred on the receptive field of the unit, and stimulated the 'on' centre, but not the 'off' periphery. The background was 20° in diameter, and extended well beyond the receptive field of the unit, both centre and periphery. The

background was on continuously, and the spot was turned on for 1 sec at intervals of approximately 5 sec.

The filled circles in Fig. 2 are the experimental points for a blue spot of 480 nm against an orange background of 590 nm. The dashed curve has been drawn by hand through them, and will be shown to be the increment threshold curve for the rods. The continuous curve is the increment threshold curve for the cones, obtained from Fig. 3 and transposed sideways

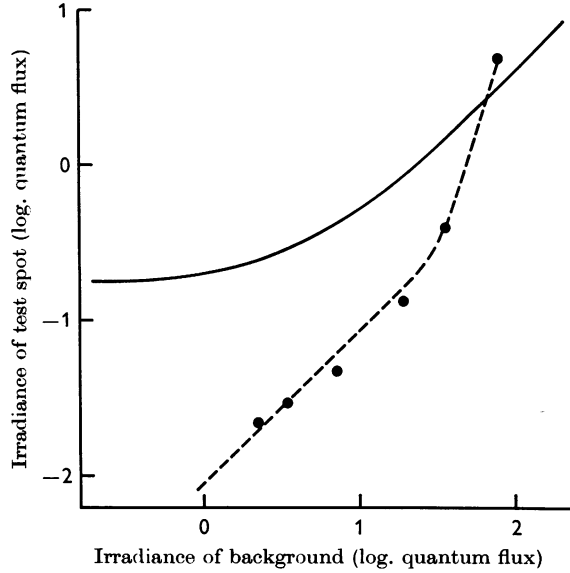

Fig. 2. Increment threshold for 1½° spot of wave-length 480 nm (blue), against a 20° background of wave-length 590 nm (orange). Spot centred in receptive field of unit. Dashed curve drawn by hand. Continuous curve taken from Fig. 3, which describes the same unit, after a transposition determined by Table 1.

and upwards by the values given in Table 1 for cat photopic vision. Taking for granted for the moment that the dashed curve really does represent the increment threshold for rods, the rods are seen to saturate when the orange background is 1·5 log. units or more of quantum flux.

Figure 3 shows the increment threshold for an orange spot of 590 nm against a blue background of 480 nm. The circles are the experimental points, and the continuous curve has been drawn through them by hand. The results show a definite threshold value of −1 log. quantum flux of 590 nm for the process represented by the continuous curve, which will be shown to be the cone process. The dashed curve comes from Fig. 2. It has been transposed according to the spectral sensitivity for cat scotopic vision (1·17 log. unit leftwards for change in background from 590 to 480 nm, and 1·17 log. unit upwards for change in test spot from 480 to 590 nm:

see Table 1). The fit of the dashed curve to the experimental points after transposition is one piece of evidence that the dashed curve represents a process with spectral sensitivity peaking at 500 nm, i.e. the rods.

In the next experiment we measured increment thresholds for a white spot against a white background. Both spot and background were the same size as before, and had the same timing. The results are given by the

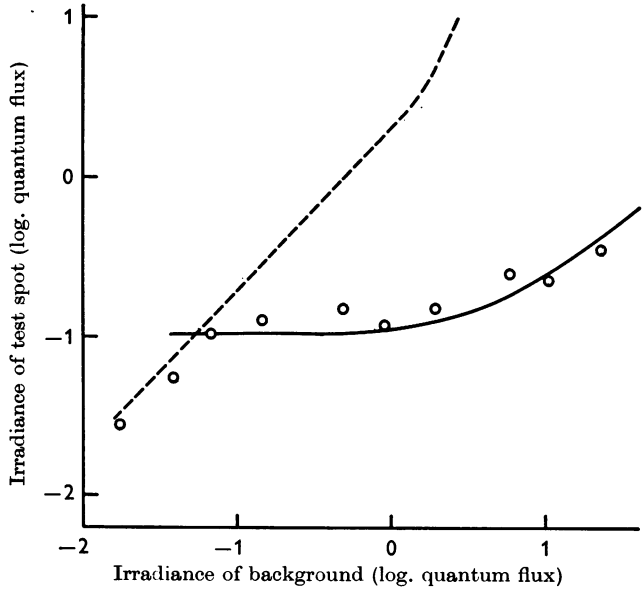

Fig. 3. Increment threshold for 1½° spot of wave-length 590 nm (orange), against a 20° background of wave-length 480 nm (blue). Spot centred in receptive field of unit. Solid curve drawn by hand. Dashed curve taken from Fig. 2, which describes the same unit, after a transposition determined by Table 1.

filled circles of Fig. 4. The continuous curve comes from Fig. 3 after transpositions according to the spectral sensitivity for cat photopic vision (0·12 log. units down and 0·34 log. units left: see Table 1). The dashed curve comes from Fig. 2 after transpositions according to the spectral sensitivity for cat scotopic vision (0·57 log. units up and 0·60 log. units left: see Table 1). The fit of the curves to the experimental points is further evidence that the continuous curve represents the cones and the dashed curve the rods.

Finally, increment thresholds were measured for six wave-lengths against four different intensities of white background. The results are described by Fig. 5 for backgrounds of −0·8, 0·2, 1·0 and 2·1 log. cd/m². The continuous curves in Fig. 5 are the spectral sensitivity of cat photopic vision peaking at 556 nm (see Fig. 10) and their positions were determined

by the continuous curve of Fig. 4. The relative positions of the continuous curves in Fig. 5 may be readily estimated by looking from Fig. 4 to Fig. 5. For example, Fig. 4 shows that the thresholds for the cones against backgrounds of $-0{\cdot}8$ and $0{\cdot}2$ cd/m^2 are close together, and the two continuous curves in Fig. 5 for these two intensities of background are correspondingly close together. Moreover, the absolute positions of the curves in Fig. 5 may be calculated from Fig. 4 as well. In fact the trough of each of the

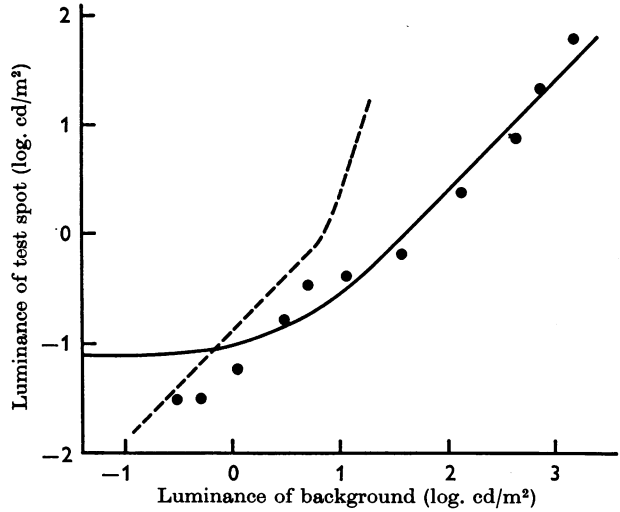

Fig. 4. Points give increment thresholds for a $1\frac{1}{2}°$ white spot against a 20° white background. Spot centred in receptive field of unit. Continuous curve taken from Fig. 3, and dashed curve from Fig. 2, which describe the same unit, after a transposition determined by Table 1.

continuous curves in Fig. 5 falls at the same numerical value as the corresponding threshold in Fig. 4 because 0 log. cd/m^2 is equivalent to 0 log. quantum flux of 556 nm for cat photopic vision; Fig. 4 gives the threshold for white light, while the troughs of the solid curves in Fig. 5 give the threshold for 556 nm. Consequently the fit of the curves to the points in Fig. 5 gives two pieces of evidence that the continuous increment threshold curve represents the cones. One piece of evidence is that the spectral sensitivity curve, peaking at 556 nm, is a reasonable fit to the experimental points. The other piece of evidence is that when the positions of the continuous curves were determined by a calculation which assumed a spectral sensitivity peaking at 556 nm, the curves fell on the experimental points.

Similar statements hold for the dashed curves of Fig. 5. They are the Dartnall nomogram for a pigment peaking at 500 nm. The fit of the curve to the points suggests that the rods are involved for the same two reasons:

(i) a curve peaking at 500 nm fits; and (ii) the positions of the curves were calculated from the dashed increment threshold curve by assuming a spectral sensitivity peaking at 500 nm.

The results of Figs. 2–5 were all obtained from the same unit. The complete series of measurements was done on three other units, with similar results. In addition, a series of increment threshold curves was measured on several other units. For example, the thresholds for a white spot on

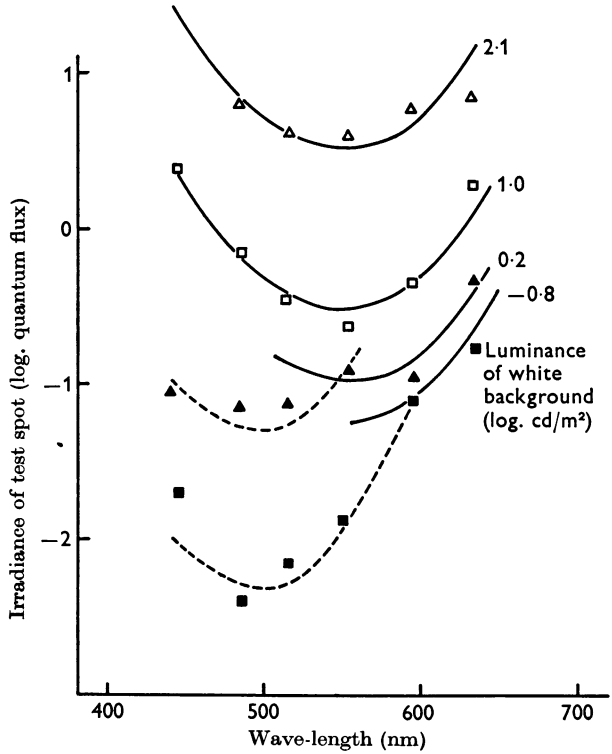

Fig. 5. Points give increment thresholds for 1½° spot of various wave-lengths against a white background of various intensities (spot centred in receptive field). Continuous curves are the average cone curve from Fig. 10; dashed curves are the Dartnall nomogram for 500 nm. The vertical position of all the curves is determined from Fig. 4, which describes the same unit.

510 nm backgrounds were compared with the thresholds for a 590 nm spot on 510 nm background. The results were always predicted by the spectral sensitivity of the rods, the spectral sensitivity of the cones, or both. All units studied were found to have both rod and cone input.

In summary, all thresholds measured in the mesopic region can be explained in terms of two processes. One is a rod, or scotopic, process, with spectral sensitivity peaking at 500 nm, and increment threshold described

by the dashed curve. The other is a cone, or photopic process, with spectral sensitivity peaking at 556 nm, and increment threshold described by the continuous curve. Anywhere in the mesopic range the more sensitive process determines the threshold. The increment threshold for a spot of any wave-length against a background of any other wave-length can be predicted from the spectral sensitivities and increment threshold curves of the two processes.

Centre compared to periphery of receptive fields. The results described so far have dealt with the threshold for a spot of the size of the centre of the receptive field. It is important to know whether the periphery of the receptive field behaves in the same way. Does the change over from scotopic to photopic vision occur at the same level in both centre and periphery? One would expect the answer to be yes from the experiments of Barlow, Fitzhugh & Kuffler (1957*b*). They showed that the area-threshold curves for red light done at photopic, scotopic and one intermediate level are all parallel to the area-threshold curves for blue light at the same level.

We investigated the question by measuring the threshold for several wave-lengths against white backgrounds of various intensities, in both centre and periphery of the receptive field. Figure 6 gives the results for one unit. The backgrounds covered the whole of the receptive field, and were continuously on. The less intense background had luminance 0·05 log. cd/m^2, the more intense 1·0 log. cd/m^2. Thresholds were measured for seven wave-lengths for a $1\frac{1}{2}°$ spot, and for a $1\frac{1}{2}°$–12° annulus, both centred on the receptive field of the unit. The letters C give the results for the centre, the letters P for the periphery.

With this particular unit, the threshold in the centre was approximately the same as the threshold in the periphery. This was true for all wave-lengths, against both backgrounds, so that spectral sensitivity for centre and periphery were the same at all levels. Moreover, the results for the higher background were fitted quite well by the curve for cat photopic vision (Fig. 10). The results for the lower background were fitted by the envelope of the curves for cat photopic and scotopic vision, with perhaps some summation at the overlap of the curves. This suggests that the change over from scotopic to photopic vision does occur at the same level in both centre and periphery. The experiment was repeated on ten units with similar results.

Cone threshold and rod saturation. The second half of this paper will be concerned with experiments in which a white background is turned on to saturate the rods. It is therefore important to know the intensity of background at which rod saturation occurs, and how much this varies from unit to unit. Cone threshold was also determined in order to define the extent of the mesopic range.

Cone threshold was usually measured in terms of cd/m² for a spot fitting the centre of the receptive field. Two methods were used. In the first method, a substantial percentage of visual pigment was bleached by turning on the full intensity of the projector for 5 min. The light was then turned off and the dark adaptation curve was determined. In the second method, the increment threshold was measured for a spot against a 480 or 510 nm background. If the spot was white, the threshold was given directly

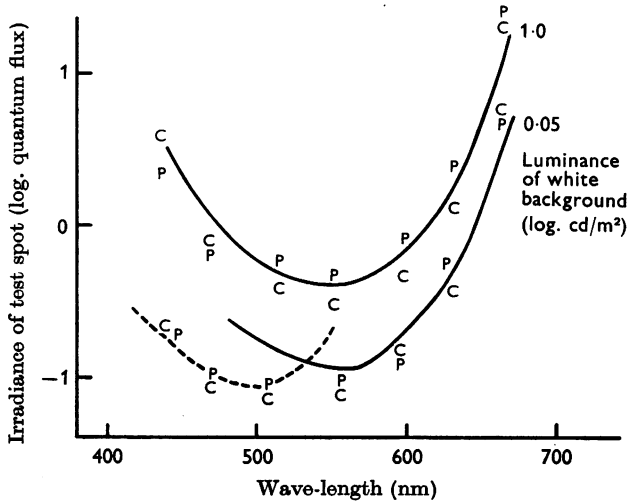

Fig. 6. Thresholds for a 1½° spot (points C) and a 1½°–12° annulus (points P), both centred on the receptive field, against a 15° white background. Continuous curves are taken from Fig. 10, for the average cone curve. Dashed curve is the Dartnall nomogram for 500 nm.

in log. cd/m²; if it was coloured, the result was corrected from quantum flux to the equivalent number of cd/m² of white light by Table 1. As predicted by experiments on humans (Crawford, 1947; du Croz & Rushton, 1966) these two methods of determining cone threshold give the same result (see Fig. 7). Cone threshold was measured for thirteen units by one or both of these methods and found to be $-1{\cdot}0 \pm 0{\cdot}4$ log. cd/m².

The intensity of background which saturates the rods was measured from increment threshold curves, the criterion for rod saturation being a slope significantly greater than 1. Usually these were threshold measurements for a spot of 480 nm against a background of 590 nm (see Fig. 2). It is also possible to observe rod saturation in the cat with blue test spots against a white background (see Fig. 4), and some results were obtained in this way. All results were converted into cd/m² of white light, according to Table 1.

Unlike cone threshold for any given unit, the intensity of background

that saturates the rods is not a clear-cut point. For the human the slope of the increment threshold curve, or the Weber fraction, starts to increase at about 2·5 log. scotopic trolands, but does not reach infinity, as it should for complete saturation, before the cone mechanism comes in at about 3 log. scotopic trolands (Aguilar & Stiles, 1954). The same is true for the cat. For most units, the Weber fraction started to increase with a level of

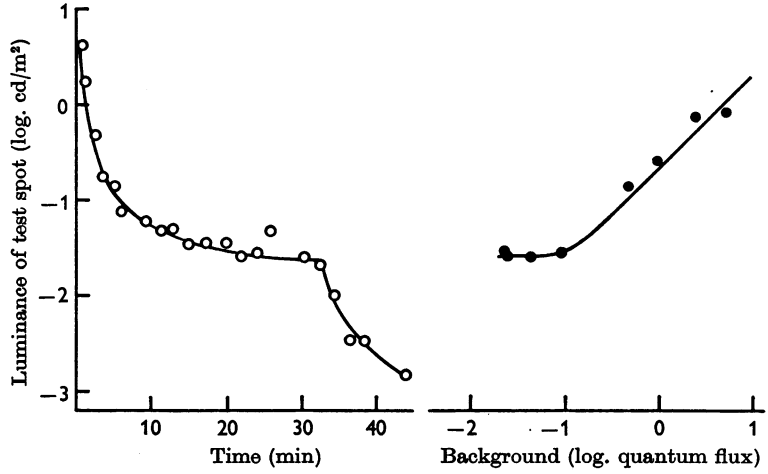

Fig. 7. Left. Dark adaptation curve after a bleach of 3000 cd/m² for 5 min. Test is a 1¾° white spot centred on receptive field. Right. Same unit, increment threshold for 1¾° white spot against a 20° background of 510 nm. Spot centred on receptive field.

background of 0·5–1·0 log. cd/m². In all units, the slope of the rod increment threshold curve was greater than 1 with a background of 1·5 log. cd/m². Therefore, in order to saturate the rods substantially in all units a background somewhat more intense than 1·5 log. cd/m² is required.

PART II. PHOTOPIC VISION

The results in the first part of this paper indicate the background necessary to saturate the rods. It was found that 1·5 log. cd/m² was always sufficient to give some degree of saturation; in all cases 2 log. cd/m² saturated the rods with a margin of safety. It is quite easy to calculate what flux of a wave-length or band of wave-lengths is equivalent to this from the spectral sensitivity of the rods. This enables us to keep the rods saturated, while varying the colour of the background, to see if chromatic adaptation will alter the spectral sensitivity of the cones.

Initially we used a white background to saturate the rods, and superimposed red, green or blue backgrounds. Three projectors were used, one

for the test spot, one for the white background, and one for the superimposed colour. The filters for the coloured backgrounds were Kodak Wrattens, no. 24 for red, no. 58 for green and no. 47 for blue. The background projectors were on continuously, and the test spot was turned on for 1 sec at intervals of approximately 5 sec.

Figure 8 gives the results from one unit in which thresholds were measured for eleven wave-lengths spaced from 440 to 665 nm, against the four backgrounds mentioned above. The test spot was 2° in diameter, and

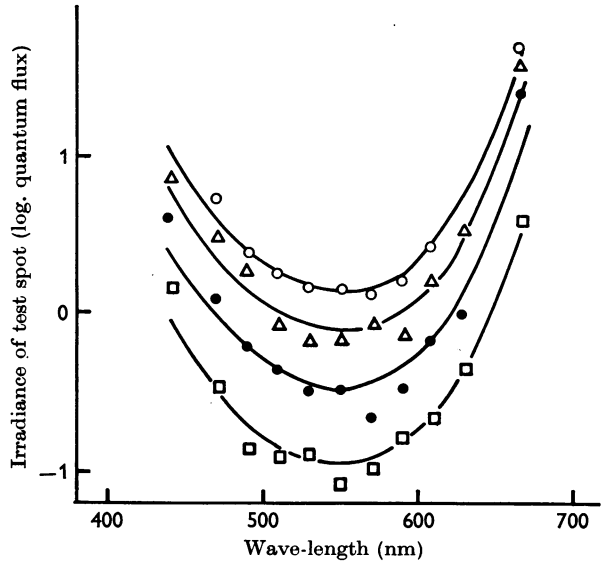

Fig. 8. Increment thresholds for a 2° spot against a 15° white background (squares) and against additional blue (filled circles), red (triangles) or green (open circles) backgrounds superimposed on the white. The four curves are identical, taken from Fig. 10, and displaced vertically to fit the relevant set of points.

the background 15°. The open squares give the thresholds against a white background, and other symbols give thresholds when a coloured background was used in addition. The four curves are all the same shape, displaced vertically to fit the relevant set of points, and are the average curve for cat photopic vision (Fig. 10). The fit of the points to the curves shows that the chromatic adaptation has not shifted the spectral sensitivity at all. The experiment was repeated on fourteen other lateral geniculate units with similar results.

In a number of other experiments, yellow and blue backgrounds were used, without any white background. The yellow filter was Kodak Wratten no. 12, chosen to provide maximum differentiation between the 556 nm cones, and any blue cones which might be present, while still

bright enough to saturate the rods. The blue filter was Kodak Wratten no. 45A, chosen to provide maximum differentiation between the 556 nm cones and any red cones which might be present and also bright enough to saturate the rods.

A typical result, from a single unit, is pictured in Fig. 9. The test spot was a $1\frac{1}{2}°$ spot, covering the centre of the receptive field, and the background had a diameter of 15°. As before, the background was on continuously and the spot was flashed for 1 sec at 5 sec intervals. Squares

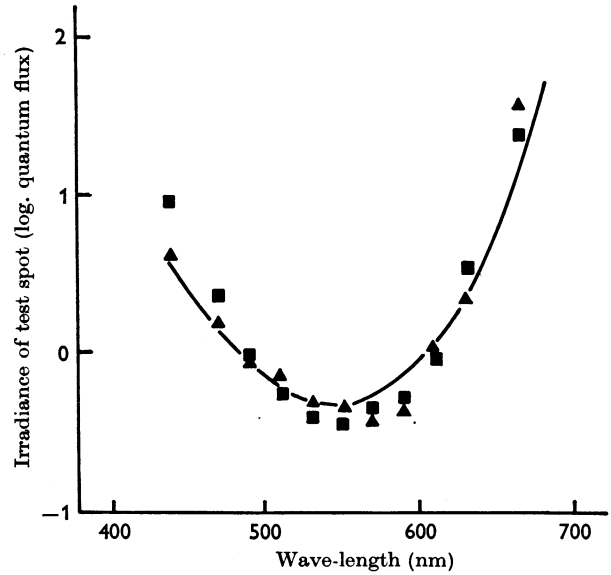

Fig. 9. Increment threshold for a $1\frac{1}{2}°$ spot, centred in the receptive field, against a 15° coloured background. Triangles: blue background (Wratten no. 45 A); squares: yellow background (Wratten no. 12). Thresholds against the blue background have been raised 0·3 log. unit to facilitate comparison. Curve is taken from Fig. 10, for the average cone curve.

give the thresholds against the yellow background, and triangles give the thresholds against the blue background, raised by 0·3 log. unit to facilitate comparison. The spectral sensitivity is the same in both cases, within experimental error, and fits the curve for cat photopic vision. This experiment was repeated on another twenty-four units in lateral geniculate and optic tract, with similar results. In some cases the test spot covered only the centre of the receptive field, and in other cases it covered part or all of the periphery as well.

The curve for cat photopic vision can now be illustrated. We have established that it is a curve for the cones, without any contamination by the rods, and also that it represents a series of curves which all peak at

approximately the same wave-length, and all have approximately the same shape. (Some variation is to be expected, since the colour of the cat's tapetum varies from one part of the retina to another, and from one animal to another (Weale, 1953*a*).) The points in Fig. 10 represent the mean of measurements on sixty-four different units and the vertical bars give the standard deviations. The continuous curve was drawn by hand through the points, and is the curve used in Figs. 5, 7, 8 and 9 and for Table 1. The

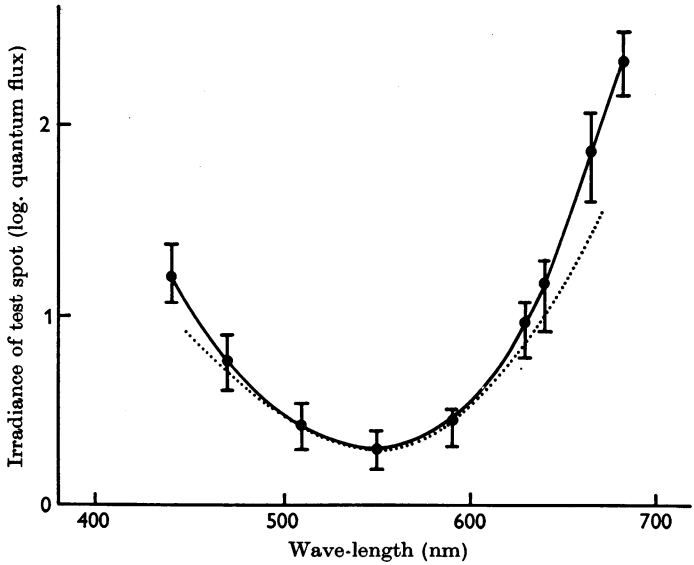

Fig. 10. Thresholds for nine wave-lengths against a background sufficient to saturate the rods. Mean of measurements on sixty-four units. Bars give standard deviation of measurements. Continuous curve drawn by hand. Dotted curve is the Dartnall nomogram for 556 nm.

dotted curve is the Dartnall nomogram for a visual pigment peaking at 556 nm, and it is noticeable that it is wider than the continuous curve, falling outside the standard deviation of the measurements at both ends of the spectrum (see Discussion).

Distribution of units and the size of their receptive fields. A record was kept of the position of the units in the lateral geniculate or optic tract, the position of their receptive fields in the cat's visual field and the size of the centre of the receptive field. Optic-tract axons were distinguished from lateral geniculate cells according to the criteria described by Hubel (1960) with subsequent confirmation from the histology. A total of eighty-one units were studied; fifty-one were in the lateral geniculate, four in the optic radiations just above the geniculate, and twenty-six in the optic tract. In the lateral geniculate, sixteen were in layer A, sixteen were in

layer A-1 and sixteen were in layer B. There were three lateral geniculate units whose anatomical position was unclear. The centre of the receptive fields of the units ranged in size from $\frac{1}{2}°$ to $2\frac{1}{2}°$.

The position of the receptive fields of these units is illustrated by Fig. 11. Since all recordings were made from the right lateral geniculate and optic tract, all receptive fields were in the left visual field. Both central and

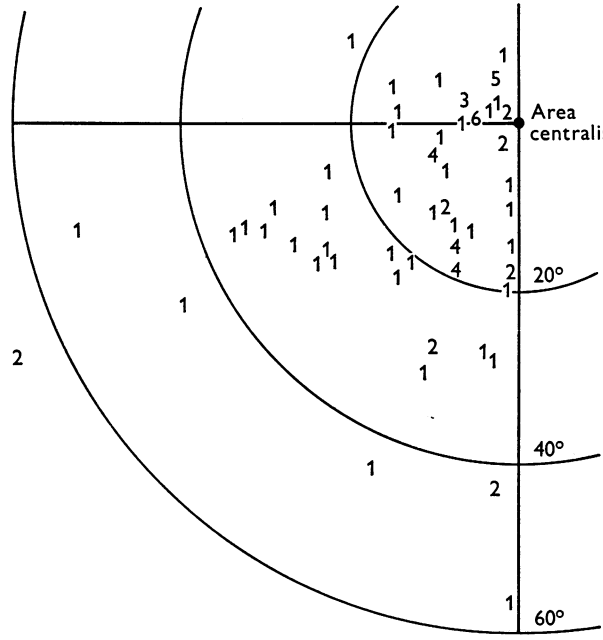

Fig. 11. Positions of receptive field centres in the cat's visual field. Numbers represent the number of optic tract fibres or lateral geniculate cells studied at the indicated visual field position.

peripheral regions of the retina were well represented. We did not detect any differences, as far as the points in this paper are concerned, between optic tract and lateral geniculate, between one layer of the lateral geniculate and another, between central and peripheral regions of the retina, or between large and small receptive field centre sizes.

DISCUSSION

All single units recorded in the lateral geniculate and optic tract of the cat have two basic spectral sensitivities, namely a scotopic spectral sensitivity operating at low levels, and a photopic spectral sensitivity operating at high levels. The change over from scotopic to photopic spectral sensitivity is gradual, and takes place at approximately the same level in the centre

and periphery of the receptive field of a unit. The photopic spectral sensitivity cannot be shifted by chromatic adaptation if the rods are saturated. Thus the system is quite different from that in the monkey lateral geniculate (Wiesel & Hubel, 1966). There is no evidence in the cat of opponent cone processes, or even of rods and cones feeding into a single unit in an opponent manner.

The photopic spectral sensitivity is narrower than the Dartnall nomogram for a visual pigment with the same peak wave-length. This is to be expected from previous work on both difference spectra and action spectra of cone pigments measured *in vivo* (Arden & Tansley, 1955; Weale, 1955; Rushton, 1959; Stiles, 1959). In addition the cat tapetum reflects more light in the middle of the spectrum (Weale, 1953*a*), which should increase the sensitivity to those wave-lengths by some factor less than 1·6. The fact that the photopic spectral sensitivity is not wider than the Dartnall nomogram lends further support to the hypothesis that only one type of cone is feeding into these units.

In the mesopic region the thresholds were predicted quite well by Stiles' hypothesis of independent mechanisms (Stiles, 1944; Bridgman, 1953). According to this hypothesis, the threshold is determined by the most sensitive mechanism. At points where two mechanisms have approximately equal sensitivity, one might expect the threshold to be lower than that predicted by the envelope of the sensitivity curves, due to summation. Our measurements did not show the difference of 0·3 log. units, predicted by full summation for points of equal sensitivity. More exact measurements would be required to find the smaller difference predicted by a probability summation.

Rod saturation occurs at approximately the same intensity of background as it does in humans. In our experiments the Weber fraction started to increase with a background of about 3 cd/m^2, which would be approximately 30 cd/m^2 seen through a natural pupil. The rods of the human start to saturate with a background of 15 cd/m^2 (Aguilar & Stiles, 1954). Cone threshold, on the other hand, is much higher for single units of the cat lateral geniculate than it is for psychophysical measurements in the human. The value for the cat is 0·1 to 2·5 cd/m^2, whereas the value for the human is 0·003 cd/m^2 (Pirenne, 1961*b*), both values given for the natural pupil. The difference in values for cone threshold may be partly, but not entirely, explained by the difference in the nature of the measurements. It is likely, therefore, that the mesopic range is narrower for the cat than for the human. The higher cone threshold probably explains the fact that rod saturation can be observed against a white background in the cat (see Fig. 4), but not in the human.

Nearly all of this is consistent with Granit's observations (1943, 1945,

1947) although not with his interpretation of them. Granit's modulators were obtained by subtracting the visual purple curve from his various spectral sensitivities. It is easy to obtain red and green modulators by subtracting the visual purple curve from the spectral sensitivities shown for the mesopic range in this paper. The blue modulator is harder to produce, but it can be done with some assumptions, such as a receptive field boundary which is not in the same place for rods and cones and a test spot which straddles the boundary between centre and periphery of the receptive field. This explanation of Granit's results would help one to understand why the colour of his chromatic adaptation did not always differ from the colour of the modulator produced: four of his nine green modulators were produced with green adaptation, the reverse of what one would expect. One observation that we have no explanation for at the moment is that one third of Granit's units had no cone input, whereas all of ours had cone input.

Nevertheless, our results are not conclusive for the existence of a single type of cone in the cat. Several possibilities for error remain. One is that the cat has several types of cones, but that they project to the tectum rather than the lateral geniculate, and were missed because of a small sample of optic tract fibres. This seems unlikely from comparative neurophysiology. In all animals where both tectum and diencephalon have been carefully studied, colour information goes to the diencephalon, but not the tectum (Muntz, 1962; Michael, 1968). Another possibility is that there are several types of cones feeding into each lateral geniculate cell, but that all except the 556 nm type have such a small influence that they were not detectable by our methods. If this is true, it is a poor basis for colour vision. A third possibility is that only a small proportion of lateral geniculate cells have input from cones other than the 556 nm type, and that our sample did not include any of them.

If the cat does distinguish wave-lengths by using rods and a single type of cone, then one should be able to test this behaviourally. The information about rod saturation given in this paper provides the knowledge necessary to design the experiment. We are now training cats to discriminate wavelength, with the intention of finding out if they retain this ability at high levels of light adaptation.

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