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# CONE SIGNALS IN THE CAT'S RETINA

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SUMMARY

1. The discharges of ganglion cells in the cat's retina were recorded under conditions intended to isolate the cone system.

2. Stiles' two-colour threshold technique permitted the photopic system to be studied when at its highest sensitivity. The absolute sensitivity of a ganglion cell, expressed in equivalent photons of $\lambda_{max}$ at the *cornea* per impulse discharged, was about 2500 times less when driven by cones than when driven by rods. This ratio improves to around 200 when allowance is made for the much smaller fraction absorbed by cones of photons incident on the cornea.

3. The number of extra impulses discharged in response to a brief flash was approximately proportional to the number of photons in the flash, up to a limit.

4. There was a region in the middle of the receptive field within which the area of a test spot and its illumination for threshold varied inversely. A flash extending over the peripheral part of the receptive field raised threshold above its minimum, presumably as a result of surround antagonism. Assessed from area–threshold curves, the balance of centre-surround antagonism in the photopic receptive field did not seem to depend upon background illumination.

5. The threshold for a small (0·2°) flash confined to the middle of the receptive field was independent of background illumination until the background exceeded a particular level, the 'dark light' ($I_o$). In different units this ranged about a mean of 7·89 log photons (560 nm equivalent) $deg^{-2}$ $sec^{-1}$. For backgrounds that exceeded $I_o$, threshold followed approximately Weber's law up to the highest illuminations that could be produced.

6. With test flashes that *filled* the centre of the receptive field, the

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Weber fraction (test flash illumination/background illumination) in some units fell below 1%.

7. Changes in the time course and latency of response accompanied the changes in sensitivity caused by alterations in background illumination. Responses of both *X*- and *Y*-cells became more transient and faster.

8. The loss of sensitivity to a test flash brought about by a steady background light depended upon the size of that light. Sensitivity varied inversely with background area within a central region that matched closely the summing area for test flashes.

## INTRODUCTION

The scotopic behaviour of the cat's ganglion cells is well documented, but there exists no similarly detailed picture of photopic behaviour, probably because the cells are quite insensitive to lights that excite cones, and observations are correspondingly difficult to make (Daw & Pearlman, 1969). For the experiments of the following paper, which examine the behaviour of a ganglion cell when it may be driven by both rods and cones, we had to be able selectively to stimulate the rod and cone systems. The aim of this paper is to show under what conditions the rod and cone systems may be isolated in ganglion cells, and to describe the behaviour of these cells when driven by cones.

It was found that, although the photopic system is less sensitive, in all important respects ganglion cells when driven by cones behave as they do when driven by rods: sensitivity to a test flash presented upon the middle of the receptive field depends upon the size of the flash; sensitivity is reduced by the presence of steady backgrounds and depends upon both background size and illumination which, within limits, may be varied reciprocally for constant effect; the discharge patterns are sustained at low background illuminations and become transient at high.

## METHODS

*Preparation and recording.* Adult cats were anaesthetized initially with an injection of ketamine hydrochloride (Vetalar, 20–25 mg/kg I.M.) and surgical anaesthesia was maintained by ultra short-lasting barbiturate, sodium thiamylal (Surital), given I.V. In some cats anaesthesia was induced by I.V. injection of Surital. During the experiments animals were kept lightly anaesthetized with urethane given I.V. (an initial dose of 200 mg/kg, given over a period of 2 hr during surgery, succeeded by a regular infusion at 10–20 mg/kg.hr). The cervical sympathetic trunk was cut bilaterally, and cats were paralysed with a mixture of gallamine triethiodide (Flaxedil, 10 mg/kg.hr) and diallylnortoxiferine dichloride (Alloferin, 1 mg/kg.hr). Expired $CO_2$ was measured continuously and, if necessary, adjustments were made in the rate of the respiration pump which otherwise was set to give 25 strokes/min at a tidal volume set according to the cat's weight. Heart rate

and mean arterial blood pressure also were monitored. In most cats blood pressure in the region of 120 mmHg was maintained indefinitely, but in a few methoxamine hydrochloride (Vasoxyl) in 25–50% glucose, given I.V., was required to prevent blood pressure falling below 90 mmHg. The eyes were atropinized and the nictitating membranes were retracted by the application of phenylephrine hydrochloride. Transparent contact lenses of appropriate power made the eyes emmetropic. No artificial pupils were used, as all light entering the eye was contained in a pencil of rays which formed a small (4 × 1 mm) image of a filament in the plane of the pupil. This allowed great depth of field.

Action potentials, recorded from single optic tract fibres with lacquered tungsten micro-electrodes (Hubel, 1957) were amplified, played through a loudspeaker, displayed on an oscilloscope and recorded on magnetic tape. The mean rate of discharge was traced continuously by a heavily damped pen-recorder.

The results in this paper and the next are based upon records from forty-six cells in twelve cats, of which twenty-eight units provided detailed information. All but two of the units studied in detail had on-centre receptive fields; off-centre units generally were avoided because it was hard to determine thresholds for brief incremental flashes. Nine units were *X*-cells and eleven *Y*-cells. These were distinguished by several tests, which included: (1) centre size, shape of area–threshold curves and the cell's behaviour when a narrow slit of light was moved through the receptive field at different velocities (Cleland, Levick & Sanderson, 1973); (2) the time course of responses to centrally located test spots (Cleland, Dubin & Levick, 1971; Jakiela, Enroth-Cugell & Shapley, 1976); (3) responses to the temporal modulation of a diffusely illuminated field. This test reveals two differences between *X*- and *Y*-cells. First, in the mesopic range, a threshold response from a *Y*-cell requires a modulation of 1% or less (Tobin, 1976), while the *X*-cell's threshold is considerably higher (see e.g. fig. 9, Enroth-Cugell & Robson, 1966). Secondly, as modulation is increased in small steps suddenly there appears in the response of the typical *Y*-cell (but not *X*-cell) a second discharge peak in the opposite phase of the stimulus. The remaining eight cells were not classified but had concentrically organized receptive fields.

In a few cats the position of the optic disk was determined by reversed ophthalmoscopy and the eccentricity of receptive fields therefore could be determined fairly precisely, but usually the locations of receptive fields were inferred from the presumed direction of the visual axis in the paralysed cat (Vakkur, Bishop & Kozak, 1963), in which case the estimate was probably not off by more than 5°.

*Stimulus.* A Maxwellian view optical system provides a convenient means of producing high retinal illuminations with a small effective pupil, but usually it allows only a small field of view, and is not easily aligned with the eye. Since we recorded from optic tract fibres, a system was required that could be adapted speedily for use with either eye, and which would allow stimuli to be positioned anywhere within a large region around the area centralis without need to move the animal or the entry point in the pupil. Our optical system is illustrated diagrammatically in Fig. 1. Apart from its final stages, which were designed to satisfy the above requirements, it was conventional. It provided three channels that were optically identical and transmitted light from the same tungsten filament source (an H-1 Tungsten-iodide headlamp bulb, rated at 55 W, and run at constant current from a stabilized d.c. supply). For simplicity one channel only is illustrated. A reduced image of the filament was formed upon the neutral density wedge, W (Kodak, M-type), by the lens $L_1$. In two of the channels a high-speed electromagnetic shutter (Uniblitz, Model 26, Vincent Associates, Rochester, N.Y.) was placed close to the wedge, where it could occlude the whole beam effectively at the same instant. Light was collimated by lens $L_2$, and into the resulting beam could be

inserted colour filters and additional neutral ones. The variable field-stop, A, was mounted on a carriage and could be moved vertically or horizontally across the beam, which illuminated it uniformly. The separate channels were combined in beam-splitting cubes, B (one only is shown), and the resulting beam brought to a focus by $L_3$ upon the centre of a mirror, M, which was mounted in a gymball, and could rotate in two dimensions about the centre of its front surface. $L_4$, which was close to the mirror, formed reduced images of the field stops in the focal plane of the Maxwellian lens, $L_5$. This in turn imaged the filament in the cat's pupil and the field stops at infinity. The lens (Canon, focal length 50 mm, f 0·95) provided for the observer a total field of view of 45° within which the images of the field stops (maximum subtense 15°) could be moved together by rotation of the mirror M, without any shift of the filament image in the plane of the pupil. The image of one field stop could be moved with respect to another by adjustment of the carriage upon which the stop was mounted. Test and background spots could be varied in diameter from 0·1 to 15° by adjustment of the field stops in the channels, and the duration of presentation could be varied from a minimum of 5 msec.

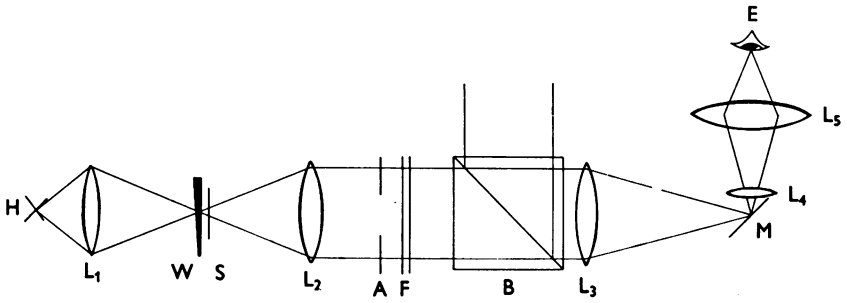


Fig. 1. The Maxwellian view optical system (not to scale). This is fully described in the text. H, source, tungsten iodide lamp; $L_1$, condenser, focal length 67 mm; W, neutral wedge; S, electromagnetic shutter; $L_2$, collimating lens, focal length 190 mm; A, aperture, diameter variable in fixed steps from 0·1 to 1·2° and thereafter continuously up to 15°; F, neutral and coloured filters; B, beam-splitting cube; $L_3$, objective, focal length 1000 mm M, front surface mirror mounted in gymballs to allow rotation about; centre of filament image; $L_4$, field lens, focal length 250 mm; $L_5$, Maxwellian lens, focal length 50 mm; E, eye.

Since the distance from the mirror to $L_5$ was relatively large, $L_5$ could be moved considerably off the optical axis of the apparatus without introducing significant aberrations. Thus, by arranging that the optical axis lay midway between the cat's eyes and approximately along the cat's line of sight, it was possible, simply by translating $L_5$ horizontally and vertically, to centre the filament image in the pupil of either eye without need to move the cat or the rest of the optical system.

All neutral filters were calibrated individually through the visible region of the spectrum in a Carey recording spectrophotometer, and checked in the apparatus with a photomultiplier in the position of the eye. The neutrality and density of the wedges were checked in the apparatus.

Experimental measurements were made using white light or, more often, with a blue-green absorption filter (Ilford 603) interposed to provide a light particularly effective for rods, and/or a deep red filter (Ilford 608) to provide light to which rods would be most insensitive. It was not necessary to know the exact spectral com-

position of these lights, since the effectiveness of each was expressed in terms of an equivalent at the wave-length of peak absorbance ($\lambda_{max}$) for the rods or for the single type of cone that contributed to the discharges recorded.

The rhodopsin in the cat's rods has an absorption spectrum with $\lambda_{max}$ close to 500 nm (Weale, 1953*b*). $\lambda_{max}$ for the predominant cone type seems to be close to 560 nm (Granit, 1943; Daw & Pearlman, 1969). Thus to calibrate our lights we established, in experiments made on ganglion cells, the scotopically equivalent monochromatic light of 500 nm and the photopically equivalent one of 560 nm.

The scotopic densities of the Ilford 603 filter (dominant wave-length 490 nm) and the 608 filter (transmits above 620 nm) were measured in the dark-adapted eye. A 0·2° test spot was centred on the receptive field and the neutral density for threshold was found with and without the coloured filter in the beam, the difference between these values being the scotopic density of the coloured filter. The photopic densities of the filters were determined in the same way, but in the presence of a background that fully saturated the rods. This ensured that the threshold stimulus acted through cones. Measurements made on 23 units gave the following mean densities ($\log_{10} \pm 1$ S.D.) for the broad band filters: Ilford 603, scotopic $= 1{\cdot}25 \pm 0{\cdot}074$; photopic $1{\cdot}92 \pm 0{\cdot}10$. Ilford 608, scotopic $= 3{\cdot}19 \pm 0{\cdot}17$; photopic $1{\cdot}96 \pm 0{\cdot}10$.

The densities of the two monochromatic filters were established in the same way, and these monochromatic lights were calibrated absolutely, as follows. The spectral energy distribution of the unfiltered source through each optical channel (with a fully open field stop) was measured with a Gamma 2020 spectro-radiometer, with the sensor in the position of the eye. The image of the source fell upon a small part of the sensor surface, so the radiant flux could be read directly. Spectral radiant flux was found to rise almost linearly with wave-length over the range 425–650 nm. From these measurements and the transmission spectra of the two calibrated interference filters (Balzars Filtra-flex B-40, half-widths about 7 nm) the total radiant flux transmitted by each filter was calculated. This flux was distributed in a disk of diameter 14·5°, so the retinal irradiance (without allowance for transmission losses in the eye) could be deduced directly. For one channel the irradiances were $1{\cdot}0 \times 10^{11}$ photons (500 nm) deg$^{-2}$ sec$^{-1}$ and $1{\cdot}6 \times 10^{11}$ photons (560 nm) deg$^{-2}$ sec$^{-1}$ respectively. The scotopic and photopic densities respectively of the 500 nm filter and the 560 nm one were known already from measurements made on ganglion cells, and so, by allowing for these densities, the visual effectiveness of the unattenuated white light could for rods be expressed as an equivalent at 500 nm ($2{\cdot}0 \times 10^{12}$ photons deg$^{-2}$ sec$^{-1}$) and for cones as an equivalent at 560 nm ($3{\cdot}2 \times 10^{12}$ photons deg$^{-2}$ sec$^{-1}$). In the second channel these values were 31% lower and in the third channel 66% lower.

*Fractions of photons absorbed.* Barlow, Levick & Yoon (1971) concluded from a detailed examination of the factors limiting the absorption of photons by rods that between 15 and 50% of the light incident on the cornea was absorbed. The measurements of Bonds & Macleod (1974), who used reflexion densitometry, suggest that 28% of the photons reaching the retina will be absorbed by rods, and we have used this relatively conservative estimate when calculating numbers of absorbed photons.

Corresponding calculations for cones are more difficult, for there are no measurements of pigment density *in vivo*. Dr R. H. Steinberg kindly measured for us the length of the outer segments of some cones from the cat's central retina. Taking an average figure of 17 $\mu$m, and assuming a pigment density of 0·015/$\mu$m, which is midway between the limits within which all photopigment densities seem to fall (Liebman, 1973), it is calculated that of the light entering a cone 44% will be absorbed on the first pass. Tapetal reflectance is 0·48 at 560 nm (Weale, 1953*a*), so a further 12% will be absorbed on the second pass. Even in the region of highest cone

density, rods greatly outnumber cones (Steinberg, Reid & Lacy, 1973) and much of the light incident on the retina never passes into cones. To deduce the fraction of retinal area occupied by cones we need to know cone density, which varies with eccentricity, and the size of the collecting surface exposed by each cone. The inner segment may act as an optical funnel (Enoch, 1963) so a value for the collecting surface may be estimated from the cross-sectional area of the inner segment, which increases with eccentricity (Chievitz, 1889; Steinberg *et al.* 1973). We assume also that ocular transmission losses arise principally in the lens, and estimate these at 25% (Weale, 1954). All these factors are put together in Table 1, and from them is estimated, for cones at different retinal eccentricities, the fraction absorbed of photons incident on the cornea.

TABLE 1. Fraction absorbed by photoreceptors of light incident on cornea

| | Eccentricity degrees | Ocular transmittance | Inner segment area ($mm^2$) | Cone density $\times mm^2$ | Fraction of retinal area occupied by cones | Fraction absorbed of light entering cone | Fraction absorbed of light incident on cornea |
|---|---|---|---|---|---|---|---|
| Cones | 0 | 0·75 | $5{\cdot}1 \times 10^{-6}$ | 26,000 | 0·13 | 0·56 | 0·056 |
| | 2·5 | | $5{\cdot}1 \times 10^{-6}$ | 14,500 | 0·074 | | 0·031 |
| | 5·0 | | $5{\cdot}9 \times 10^{-6}$ | 9,500 | 0·056 | | 0·026 |
| | 20·0 | | $7{\cdot}7 \times 10^{-6}$ | 5,000 | 0·038 | | 0·016 |
| Rods | — | | Fraction absorbed of light incident on retina–0·28 | | | | 0·21 |

The greatest uncertainty concerns the fraction absorbed of photons entering a cone. If Liebman's (1973) extreme values for pigment density (0·013/$\mu$m and 0·018/$\mu$m) are used and the length of the outer segment is allowed to vary by a factor of 2 in either direction, the least and greatest amounts absorbed differ from those given in Table 1 by a factor of less than 1·6. The effective collecting surface of a cone is unlikely to be greater than given in Table 1, and may be less, if the inner segment fails to funnel all the light into the outer segment. Thus the values given in Table 1 probably cannot underestimate the fraction absorbed by a factor of more than 1·5, and may over-estimate it by a factor of up to 2.

*Data analysis.* Action potentials triggered a generator that made rectangular pulses. Often responses to thirty presentations of a stimulus were averaged to give a post-stimulus time histogram, or a tracing of the mean pulse density, in which case the standard pulses were first smoothed with a time constant of 10 msec (Enroth-Cugell & Robson, 1966). The experimenter could also listen to the pulses through a loudspeaker. In this paper and the next, the 'threshold for detection' refers to the weakest stimulus that produced a discernible change in the discharge of pulses as they were played over the loudspeaker. The reciprocal of the threshold stimulus we define as 'sensitivity'.

## RESULTS

*Isolation of the cone system.* The cat's retina contains cones with a peak sensitivity to lights of wave-length close to 560 nm (Granit, 1943; Daw & Pearlman, 1969) and probably also, in much smaller numbers, cones

absorbing maximally light of wave-lengths near 450 nm (Gunter, 1954; Daw & Pearlman, 1970). This paper concerns only the behaviour of the cone system sensitive to longer wave-lengths, and in our experiments the colours of test and background lights were chosen so as to favour its isolation. Contributions from the blue-sensitive cones were observed neither here nor in experiments (Lennie, Hertz & Enroth-Cugell, 1976) in which saturation of the rod system was studied using red backgrounds. Signals from cones were found after the rods had become saturated, but always these came from green-sensitive cones.

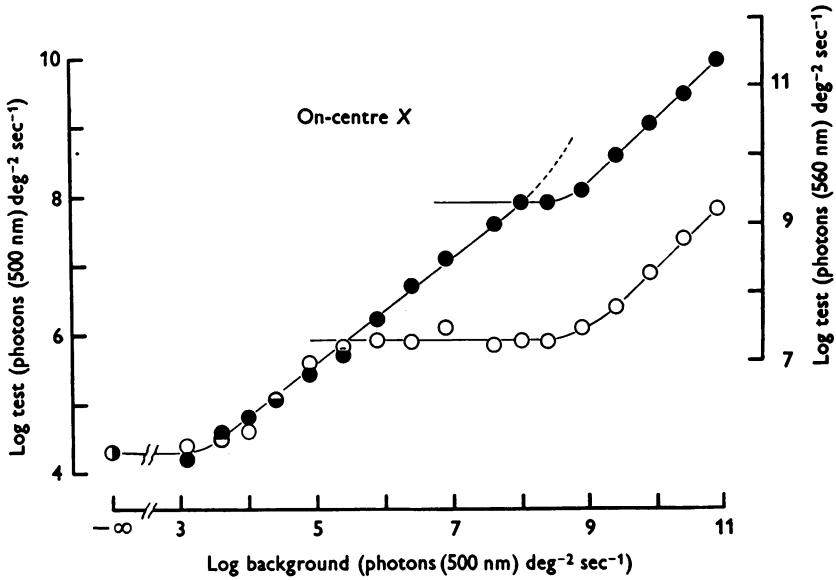


Fig. 2. Increment–threshold curves for red flashes (○) and blue-green flashes (●) presented against a blue-green background. The abscissa and left-hand ordinate give illuminations (in this as in all other Figures measured at the cornea) as numbers of photons (500 nm) calculated to be equivalent for rods to the blue-green light used. The right-hand ordinate does the same for cones, using numbers of photons of 560 nm, but this is appropriate only for the upper branch of the curve made with red flashes. The illumination of the blue-green background may be converted to photons of 560 nm by subtracting 0·45 log units from the numbers on the abscissa. Four Hz flickering test, diameter, 0·2 deg. This unit had photopic thresholds among the lowest observed. Unit 39/2.

The cone system may be isolated with a technique due to Stiles (1939) in which a short wave-length background light is used to depress the sensitivity of rods, while the cones are excited by a long wave-length light to which rods are most insensitive. Fig. 2 shows an application of this technique to a ganglion cell. The threshold for detection of a small

incremental test is plotted against the illumination of a background that covered the whole receptive field. Two tests were used, one red, the other blue-green like the background. Thresholds for both stimuli began to rise for the same background illumination and, over a range of increasing backgrounds, followed exactly the same course. This is the principal evidence that, in darkness and at low background levels, both tests were detected through rods. As the background was raised beyond $4 \times 10^5$ photons $deg^{-2}\,sec^{-1}$, threshold for the red test remained steady, while that for the blue-green one continued to rise before it too became steady. Eventually, at the highest background levels, thresholds for both stimuli resumed their upward course.

The upper horizontal branches in these increment–threshold curves appear because the test became more detectable through cones than through rods. Cones were in fact almost equally sensitive to the two lights, but because the rods were a great deal more sensitive to the blue-green than to the red, and the graph is plotted with the ordinate representing the effectiveness for rods, the cone segments are separated vertically.

It was readily verified that a red flash was being detected through cones when the increment thresholds fell along the horizontal branch of the curve (which will be referred to as the 'cone plateau'). If for the blue-green background was substituted a scotopically equal red one, threshold for a red flash rose to match that for a blue-green one, which remained unchanged. In addition, usually the time course of averaged responses to the red or blue-green test flash became quite distinguishable after the red curve had branched horizontally. This and other evidence is discussed further in the next paper. Increment–threshold curves were obtained from twenty-eight ganglion cells and none lacked a cone branch.

*Absolute sensitivity.* The position of the cone plateau on the ordinate defines the photopic absolute sensitivity, and for 25 units the absolute sensitivity to a small red flash, expressed in equivalent photons at the cornea, is in the upper part of Fig. 3 plotted against the retinal eccentricity of the receptive field. There was no clear relation between sensitivity and eccentricity, but for the nine *X*-cells log threshold was on average 0·63 units lower than for eleven *Y*-cells. There was a smaller difference (0·37 log unit) between the absolute scotopic thresholds (Fig. 3, lower). In other work from this laboratory (Jakiela *et al.* 1976) such clear differences have not been found.

By comparison with its rod system, the cat's cone system seems insensitive; in most units long wave-length test flashes were not detectable through cones until rod threshold had risen from its minimum by 1·8–2·2 log units. It is informative to compare the number of photons in a flash required by the rod and cone systems for the discharge of one extra

impulse, the quantum/spike ratio (QSR; Barlow & Levick, 1969). QSRs may be calculated if we know the number of extra impulses in a detectable response (obtained by averaging threshold responses to the test).

Threshold responses were not always averaged to permit a direct calculation of the QSR, but in a number of unpublished experiments, in which

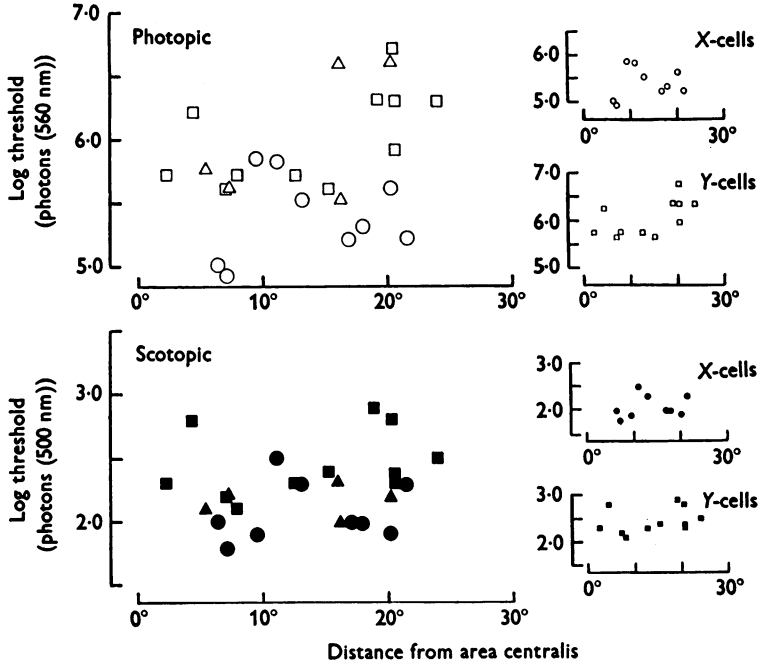


Fig. 3. Absolute thresholds, in photons per flash, for 0·2° diameter test spots flickering at 4 Hz, are plotted against the distance of the receptive field from the area centralis. Five of the twenty-five receptive fields were off the tapetum. Upper half: left graph shows, for red flashes, thresholds on the cone plateau of increment–threshold curves for *X*-cells (○), *Y*-cells (□) and cells not identified as *X* or *Y* (△). To the right, the same thresholds are plotted separately for *X*- and *Y*-cells. Lower half: as upper half, but absolute dark thresholds for blue-green flashes.

both test duration and background illumination were varied, the number of extra impulses required by the experimenter to detect the flash on half the presentations was consistently between one and three. In calculating QSRs the threshold response was assumed to be two extra impulses.

QSRs of the ten most sensitive units are given in Table 2. The values in column $QSR_c$ are based on numbers of photons at the cornea, but since cones absorb a much smaller fraction of the photons incident on the cornea (Table 1) it is useful also to calculate $QSR_r$, the number of photons

that must be absorbed for the discharge of an extra impulse. For each unit $QSR_r$ is also given in Table 2. Barlow *et al.* (1971) showed that, in the fully dark-adapted eye, the scotopic $QSR_c$ was often less than 5. The corresponding figures from Table 2 are higher, possibly because our units rarely had receptive fields in the very central retina, where the most sensitive cells are found (H. B. Barlow, personal communication).

TABLE 2. Quantum spike ratios of ten units

| Unit | Photopic $QSR_c$ | Scotopic $QSR_c$ | Ratio | Photopic $QSR_r$ | Scotopic $QSR_r$ | Ratio |
|---|---|---|---|---|---|---|
| 39/2 | 36,600 | 31·8 | 1150 | 860 | 6·68 | 129 |
| 39/4 | 144,900 | 50·7 | 2860 | 3333 | 10·65 | 313 |
| 40/4 | 144,900 | 50·7 | 2860 | 3333 | 10·65 | 313 |
| 41/1 | 115,900 | 63·5 | 1830 | 2260 | 13·3 | 170 |
| 42/1 | 29,000 | 20·0 | 1450 | 667 | 4·2 | 159 |
| 42/2 | 183,300 | 63·5 | 2890 | 3666 | 13·3 | 276 |
| 43/3 | 115,900 | 31·8 | 3640 | 2086 | 6·68 | 312 |
| 43/4 | 73,200 | 31·8 | 2300 | 1244 | 6·68 | 186 |
| 43/6 | 144,900 | 25·3 | 5730 | 2318 | 5·31 | 437 |
| 44/4 | 57,900 | 31·8 | 1820 | 1013 | 6·68 | 152 |

For explanation of QSR subscripts, see text p. 281.

The most sensitive cells had photopic $QSR_r$s of around 1000, although from cell to cell there was considerable variation – more than the variation in absolute scotopic $QSR_r$, as Table 2 shows. We think this may be due to inevitable variations from cat to cat in the entry point in the pupil which, through the Stiles–Crawford effect, would be likely to influence the photopic but not the scotopic sensitivity.

Even when allowance was made for the small fraction of photons absorbed by cones, photopic sensitivity was low – the minimum photopic $QSR_r$s usually were more than one-hundredfold greater than those for the scotopic system.

*Stimulus–response relationship.* Within some range, the number of extra impulses discharged is proportional to the illumination of an incremental test flash. This may be seen from Fig. 4 in which, for four units, the average number of extra impulses discharged during responses to a small red test flash is plotted against the number of photons (at the cornea) in the flash. The backgrounds in these experiments had been chosen to ensure that rods contributed negligibly to responses but had not lifted photopic threshold off the cone plateau (cf. Fig. 2). The response, $R$, can be described by the equation

$$R = K \log \left(1 + \frac{\Delta I}{\Delta I_0}\right), \tag{1}$$

where $\Delta I$ is the incremental flash and $\Delta I_0$ a constant that may be understood to define the range in which responses are proportional to test illumination. The line of eqn. (1), with $\Delta I = \Delta I_0$ marked by an arrow, has been drawn through the lowest set of points in Fig. 4. For this unit $I_0$ was close to threshold, but in most other units was higher. Eqn. (1) has the form of one used by Robson (1975) to relate the response of a ganglion cell to the contrast of a moving grating.

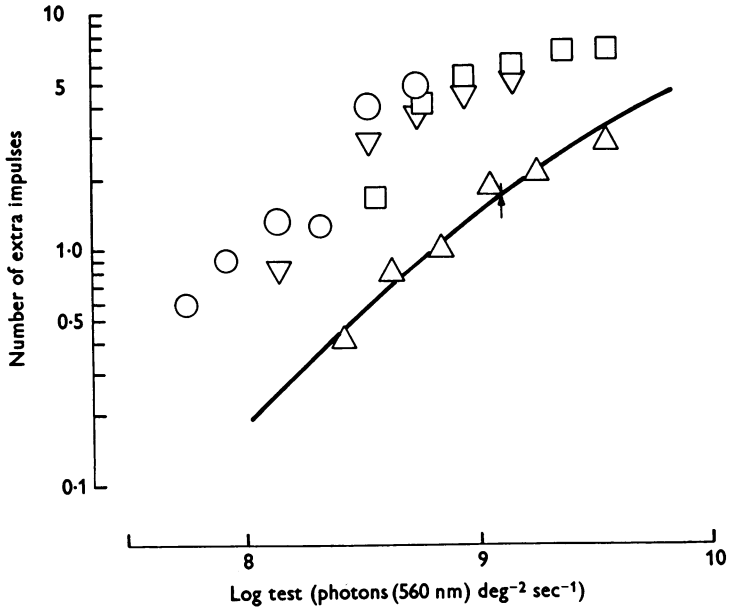


Fig. 4. Stimulus–response relation. The average number of extra impulses discharged by each of four ganglion cells following delivery of a red test flash (diameter 0·2 deg, 50 msec duration) is plotted against flash illumination. Extra impulses were measured from the average of thirty cumulative impulse counts, like the one shown in the inset to Fig. 8 and described in the text, p. 286. Almost all the extra impulses occurred within the counting period of 130 msec. The continuous line drawn through the lowest set of points is that of eqn. (1) and the vertical arrow, projected to the abscissa, shows where $\Delta I = \Delta I_0$. All observations were made using a blue-green background that exposed the cone system at its greatest sensitivity. Units: 40/4 (▽), *X*-cell; 41/3 (□), *Y*-cell; unclassified cells 43/1 (○) and 43/3 (△).

*Spatial properties of photopic receptive fields.* In the scotopic range, a ganglion cell's sensitivity to a spot briefly flashed upon the middle of its receptive field depends upon spot size. Within a limited central region, spot illumination and area may be varied reciprocally for threshold, which means that the ganglion cell responds to the total photon catch. For

flashes larger than the region of uniform sensitivity, threshold declines less steeply with area, and eventually may even rise, as test flashes encroach upon the antagonistic peripheral region of the receptive field. In photopic receptive fields, too, there is a region of spatial summation, as the following experiments show. The question of whether the regions of summation of rod and cone signals are the same is dealt with in the next paper.

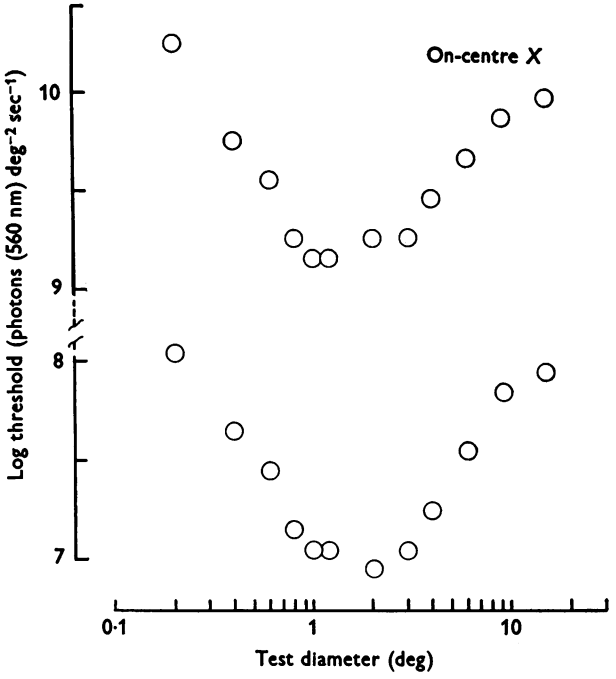


Fig. 5. Area–threshold curves made at two levels of background illumination. The lower curve was made using a blue-green background (6·4 log photons (560 nm) deg$^{-2}$ sec$^{-1}$) that kept threshold on the cone plateau, the upper curve using a background that delivered 10·4 log photons (560 nm) deg$^{-2}$ sec$^{-1}$. Flash duration 50 msec. Unit 39/2.

Fig. 5 shows, for one cell, how threshold illumination for the detection of a red 50 msec test flash varied with flash diameter at two different background illuminations (area–threshold curves were also obtained with 4 Hz stimuli). A uniform blue-green background was chosen for the observations shown in the lower curve to ensure that the flash was detected through unadapted cones and that the scotopic threshold would have been at least a factor of 10 higher. The curve resembles one that would be obtained from the fully dark-adapted receptive field, but with an interesting difference: threshold for large spots was much higher than

for optimal spots, and is interpreted to reflect antagonism from peripheral regions of the receptive field. Because of the relatively impaired sensitivity of the surround in the dark-adapted eye (Barlow, Fitzhugh & Kuffler, 1957), an area–threshold curve made in the dark-adapted eye rarely shows this steeply rising limb.

The upper graph, made upon a background that had reduced sensitivity by a little over 2 log units, is much like the lower one, and shows little evidence of change with adaptation level in the area of spatial summation or in the effectiveness of the surround.

### *Light adaptation*

Backgrounds higher than those that expose the photopic system at its fullest sensitivity reduce that sensitivity (Fig. 2). This section describes experiments to explore the mechanism of this light adaptation.

*Increment–threshold curves.* When a test flash of constant size is detected through rods, the relation between threshold illumination ($\Delta I$) and background illumination ($I$) is described by

$$\Delta I = k(I + I_0)^n, \tag{2}$$

where in these experiments, made with 4 Hz flicker, the exponent varied between 0·55 and 1·0 (about a mean of 0·78). The constant $k$ depends partly on the criterion for threshold, and $I_0$ is the 'dark-light' (see p. 289). Eqn. (2) also describes the increment–threshold curve for the cone system but the exponent $n$ (which is the slope of the straight line on the log-log plot) is higher with a mean closer to 1 (Weber's law). In a sample of twenty-two units the slope ranged from 0·7 to 1·15 with a mean of 0·93.

Changes in both time course and latency of response accompany changes in sensitivity of the cone system. Fig. 6 shows, for one $X$-cell, how the stimulus strength required for a criterion peak response of 35 impulses $sec^{-1}$ above the mean rate increases with background. The three responses included in the Figure show the transition from an entirely sustained response in the unadapted state to more transient ones as the sensitivity of the cone system was decreased. In $Y$-cells, too, cone-driven responses became increasingly transient with increasing light adaptation, but we did not determine whether responses of $Y$-cells are entirely sustained when the cone system is unadapted. When the scotopic sensitivities of $X$- and $Y$-cells are equally and moderately lowered from their unadapted levels, responses of $Y$-cells are more transient (Jakiela *et al.* 1976). This is also true of cone-driven responses. Responses of an $X$-cell and a comparably light-adapted $Y$-cell are shown in Fig. 7.

The variability of the maintained discharge makes it hard to measure latencies of individual responses and often, especially when responses are

small, it is difficult to estimate latency from pulse-density tracings of averaged responses. Latencies were measured from graphs like that shown in the inset to Fig. 8. Two graphs were drawn, each representing the cumulative average number of impulses discharged after various times from the beginning of a counting period. Open symbols show the average counts made during a period that began one half second before the presentation of a test flash; filled symbols show the counts made in a

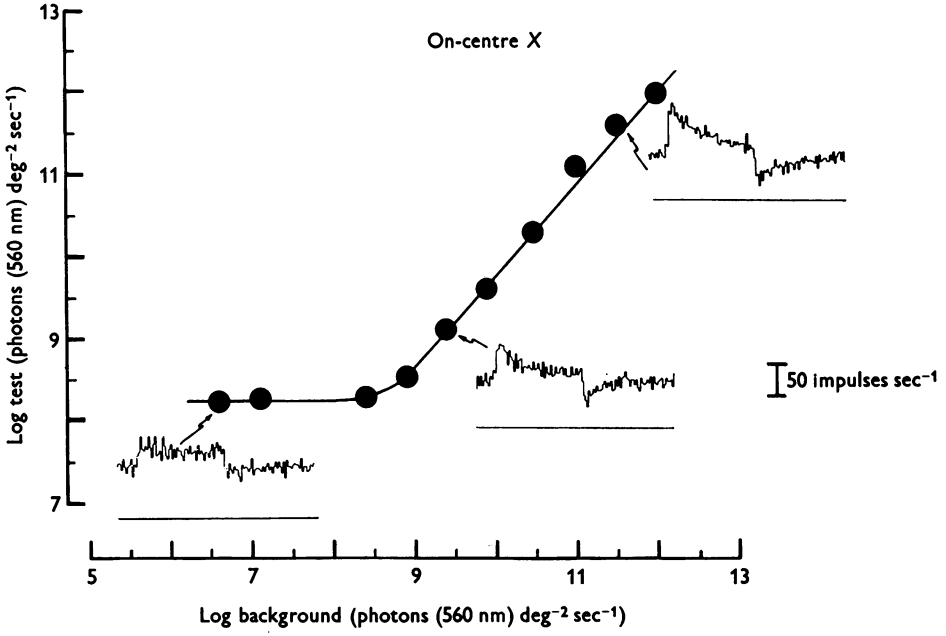


Fig. 6. Increment–threshold curve calculated from responses like those shown in the Figure, or smaller ones. The illumination required to produce a criterion peak response of 35 impulses sec$^{-1}$ above the mean rate was calculated on the assumption that responses varied linearly with illumination. Beside three of the points are drawn post-stimulus histograms of the responses from which they are derived. Note the change in time course of discharge brought about by increasing light adaptation. Unit 44/4.

period starting when the test was delivered. For some time the graphs follow the same course, then, rather abruptly, the graph of counts in the post-stimulus period diverges from the line for the discharge in the preceding period. The time of divergence, which in most measurements was sharply defined by the intersection of straight lines drawn through the two sets of points, we take as the latency. Fig. 8 shows that latency of small responses of about equal magnitude declined progressively (by about 6–7 msec per log unit) with increasing light adaptation. This is

seen in the scotopic range too (Cleland & Enroth-Cugell, 1970) but for equivalent degrees of light adaptation the scotopic latencies are longer (see next paper).

*Dependence upon background area.* In the scotopic range, sensitivity to a test light depends, within limits, upon the product of background illumination and area (the background flux) and it has been shown (Cleland & Enroth-Cugell, 1968) that the summation area for steady adapting lights,

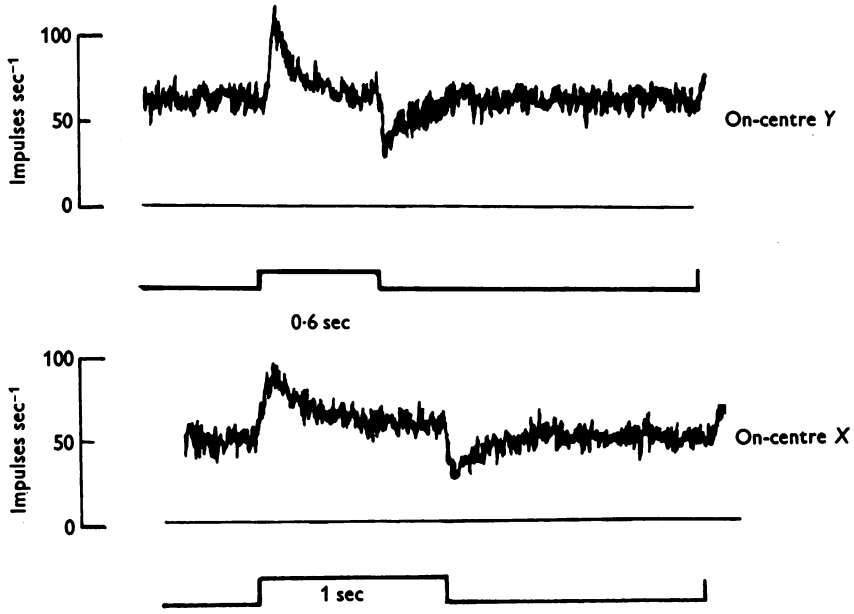


Fig. 7. Comparison of responses of *Y*- and *X*-cells that are equally light-adapted. For both units, a steady blue-green background had raised the threshold for a red stimulus to between 4 and 5 times its level on the cone plateau. The discharge from the *Y*-cell, although initially as strong as that from the *X*-cell, decayed more rapidly to a steady rate only slightly above that of the pre-stimulus period. After light offset the discharge from the *Y*-cell more rapidly returned to the steady rate. *Y*-cell 37/3, *X*-cell same unit as in Fig. 6.

the 'adaptation pool' (Rushton, 1965), matches closely the summation area ($A_t$) defined for test lights. The following experiments show that the photopic receptive field also has an adaptation pool, and that its size matches the summation area for test lights.

A steady diffuse background was chosen, from an increment–threshold curve, so as to elevate cone threshold for a small red test flash about 0·7 log unit above its unadapted level. Then threshold was found for test spots of different sizes. The resulting area–threshold function is plotted

in Fig. 9*A*. The corresponding curve (Fig. 9*B*) traces the illumination required for constant adapting effect as background size was varied. It was made by finding the background illumination that kept threshold for a small (0·2°) test flash constant at the value it had in the left-hand curve. The areas of summation revealed by both curves are the same, within the limits of measurement. Only in their expression of the effect of large spots are the curves different: that which plots threshold against test flash size

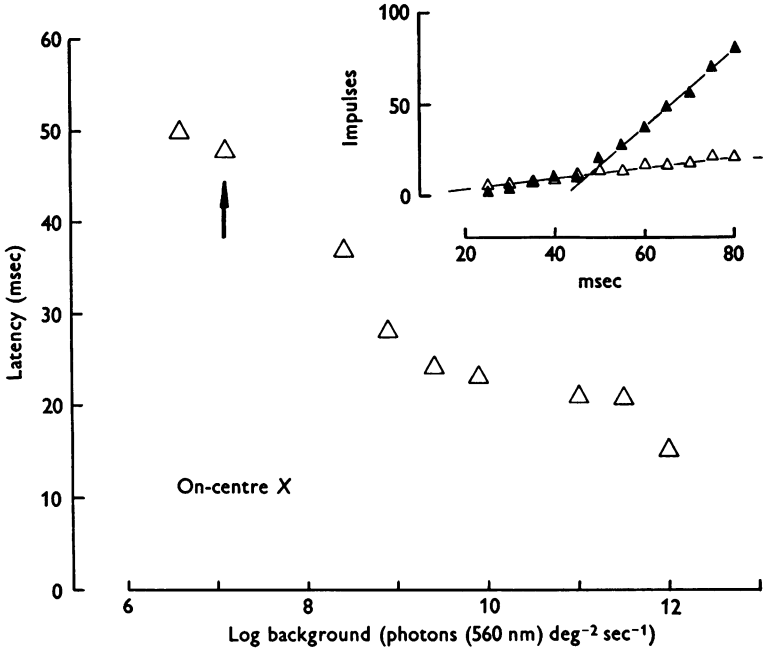


Fig. 8. Change of response latency with background illumination. Inset shows how latency was measured from the point of intersection of the two lines representing the discharge before (open symbols) and at the start of (filled symbols) the stimulus (see text, p. 286). For all the points on the main graph the small red test flash was set to give a weak response of approximately constant magnitude. Arrow indicates the latency measured from the inset. Same unit as in Fig. 6.

shows an upturn commonly found when the flashes are large enough to activate the surround, but the curve that charts the adapting effect of the background has none. This experiment was made on four cells with the same result. Thus, steady light that falls on the surround does not affect the sensitivity of the centre, a situation already shown to be the case for the scotopic system (Enroth-Cugell, Lennie & Shapley, 1975). This suggests that adaptive signals from backgrounds act upon the centre mechanism before the combination of signals from centre and surround.

*The 'dark light' of cones.* At some background illumination photopic sensitivity begins to decline from its unadapted level. One way to characterize the critical background is by the parameter $I_0$, from eqn. (2). In human psychophysics this is called the 'eigengrau' (Hering, 1925) or the 'dark light' (Barlow, 1957) by analogy with the dark current in photocells, which limits their sensitivity. Although this interpretation may not be appropriate in the context of the present experiments, $I_0$ provides a convenient way to define the background illumination that begins to reduce sensitivity. It may be estimated from the increment–threshold curve by finding the background at the intersection of the asymptotes.

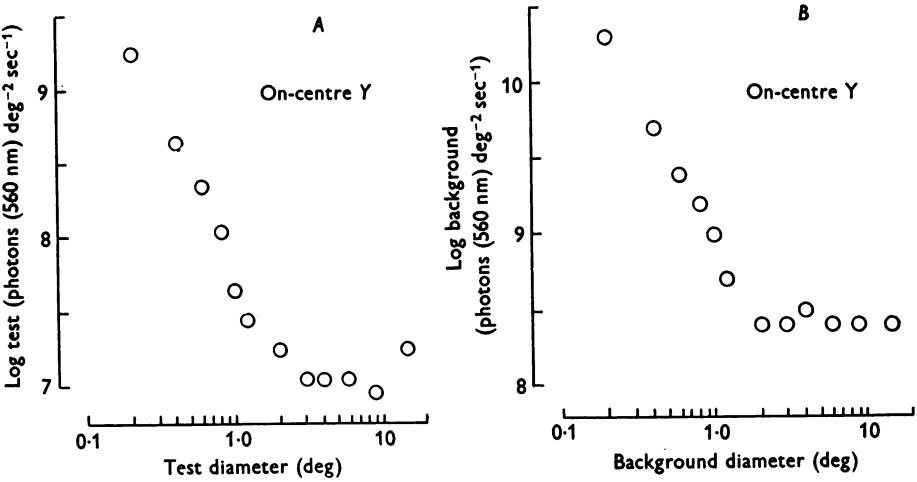


Fig. 9. *A*, area–threshold curve for a red test flash (4 Hz flicker) presented against a steady blue-green background (15 deg diameter, 8·9 log photons (560 nm) deg$^{-2}$ sec$^{-1}$) that had lifted threshold to 5 times the level of the cone plateau. *B*, area–threshold curve for the unit of *A*, but this time the test flash was always 0·2 deg diameter, with its illumination fixed to be at threshold on the 15 deg background, and the background size and illumination were then varied to keep this flash at threshold. Unit 42/2.

Log $I_0$ estimated for seventeen units had a mean of 7·89 log photons (560 nm) deg$^{-2}$ sec$^{-1}$ and a standard deviation of 0·2. For the cat's rod system the corresponding figures were 3·57 log photons (500 nm) deg$^{-2}$ sec$^{-1}$ $\pm$ 0·4 estimated for thirty-two units.

## DISCUSSION

*Absolute sensitivity.* Daw & Pearlman (1969) have measured the photopic absolute sensitivity of the cat's ganglion cells. It is hard to compare our observations with theirs, since threshold criteria may have been different,

and in their experiments light from stimuli on a tangent screen entered the eye through a dilated pupil, so some allowance must be made for Stiles–Crawford effect. An approximate correction for this may be calculated for a pupil diameter of 13·8 mm (the average value given by Vakkur & Bishop, 1963) according to a formula for human vision, given by Wyszecki & Stiles (1967), and it suggests that the radiant flux entering the eye through the fully dilated pupil might be about 5 times less effective for cones than the same flux entering the eye through a point in the centre of the pupil. If a further allowance is made for differences in size of test spots, we believe that Daw & Pearlman's most sensitive units would have had thresholds within the range of ours.

If we have correctly estimated the fraction absorbed by photoreceptors of photons incident on the cornea our results show that a ganglion cell's minimum average $QSR_r$ obtained with a small flash is around 1000 when driven by cones and about 5 when driven by rods. Thus, if rod and cone signals are processed with equal efficiency by the intervening neurones, the cat's rods are about 200 times more sensitive than its cones. Absolute flash sensitivities measured from peak hyperpolarization of photoreceptors in the turtle (Baylor & Hodgkin, 1973) and mud puppy (Fain & Dowling, 1973) show that rods are five to six times more sensitive than cones, but since the rod response lasts longer the disparity could be exaggerated at the ganglion cell. These rod/cone sensitivity ratios are from eyes generously endowed with cones and the much higher ratio found for the cat may reflect the extent to which its retina is specialized for rod vision: even in the area centralis rods outnumber cones by ten to one.

The relatively poor photopic sensitivity of the cat's retina might be thought to result from rod signals interfering with those from cones, and depressing the cone system. Steinberg (1969) suggested this to account for his observation that, while a detectable cone contribution to S-potentials recorded from the dark-adapted cat required flashes 1·0–1·5 log units stronger than a detectable rod contribution, the disparity in ganglion cells was much greater. We have no observations on the photopic system made without a steady blue-green light that strongly excited rods, but backgrounds in the range which spans the cone plateau of the increment threshold curve (Fig. 2) clearly are without effect upon photopic sensitivity, and it seems reasonable to suppose that weaker backgrounds would have acted similarly.

When measured psychophysically in cats with dilated pupils, the minimum photopic threshold for large stimuli is 6000-fold greater than the scotopic threshold (LaMotte & Brown, 1970). If allowance is made for a Stiles–Crawford effect this is close to the ratio we found (2500) for ganglion cells when small-spot sensitivities are expressed in units at the cornea.

The good agreement suggests that, in the cat's retina, the areas for spatial summation cannot be very different for rod and cone signals.

*Light adaptation.* Over the entire range of backgrounds used in our experiments the test illumination required for threshold is given by eqn. (2), even though, at the higher background illuminations, a new factor, the bleaching of cone pigments, must have contributed in some measure to the threshold. The contribution of this bleaching to the rise in threshold caused by backgrounds cannot easily be estimated for our experiments, but if bleaching signals act upon the cat's photopic system as they do upon man's (DuCroz & Rushton, 1966), the combined effect of bleaching and background upon threshold is as if the background illumination had been increased. Since bleaching increases with background illumination, the effect of it will be to raise threshold rather more the higher the background illumination. Its influence therefore could contribute to the slightly steeper slopes of photopic *vs.* scotopic increment–threshold curves, although we have insufficient information to predict the difference quantitatively.

When at its maximum photopic sensitivity, the ganglion cell discharges a relatively sustained stream of impulses in response to the prolonged presentation of a near-threshold stimulus (Fig. 6). Backgrounds that reduce sensitivity cause these averaged responses to become more transient. Similar changes are observed in the scotopic range and since, upon mesopic backgrounds, the cone response may be sustained and the rod response transient (Enroth-Cugell, Hertz & Lennie, 1977), it follows that the effect of the background upon discharge pattern must arise before the combination of rod and cone signals. That observation also rules out the possibility, already improbable on other grounds (Enroth-Cugell & Shapley, 1973), that the changes in response pattern depend upon the rate of the maintained discharge, for that discharge is different at the background levels that bring about response changes in the two systems. Thus it seems certain that, for both rod and cone systems, the changes in discharge pattern accompany the action of the gain control.

Evidently photopic sensitivity does not depend upon the extent to which backgrounds affect rods, for increases in mesopic background illumination which raise rod threshold fiftyfold leave cone sensitivity unaltered (Fig. 2). But although the photopic gain control is independent of the scotopic one, and acts at different levels of illumination, the remarkably similar effects of backgrounds upon the two systems suggest similar mechanisms of adaptation. This is curious, in view of the apparently different effects of backgrounds upon responses to flashes recorded intracellularly from rods and cones (Normann & Werblin, 1974). Responses of individual rods are, however, too small to be measured over much of

the range within which background illumination influences the increment threshold of cat's ganglion cells; it is within just that part of the range that scotopic responses from ganglion cells most resemble photopic ones.

At higher background levels the cat's scotopic and photopic systems do behave differently: the scotopic system in man (Aguilar & Stiles, 1954) and in cat (Lennie *et al.* 1976) can be rendered quite insensitive to increments ('saturated') by high background illuminations that bleach negligible fractions of photopigment. In our experiments the cone system was not saturated by any background, possibly because at the highest illumination the bleaching of pigment by steady backgrounds limits the photon catch of cones to a level less than that required for saturation (Alpern, Rushton & Torii, 1970; Boynton & Whitten, 1970).

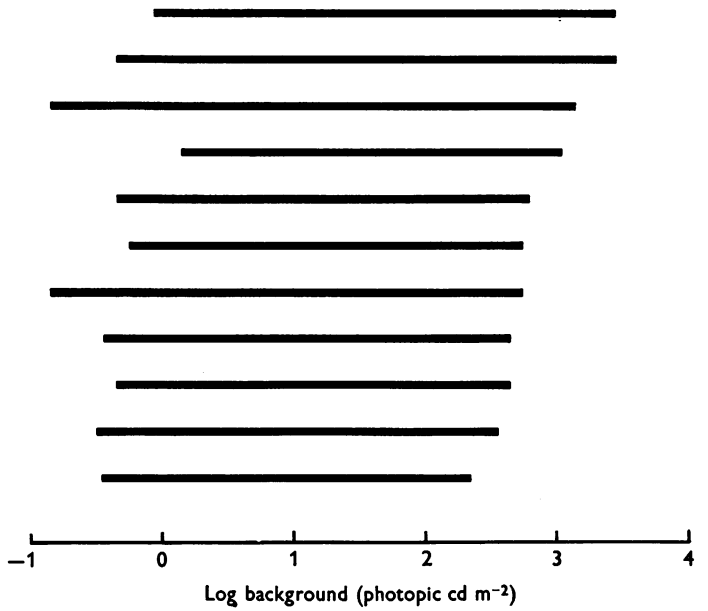


Fig. 10. The mesopic range for the cat's ganglion cells. Each horizontal bar defines for one cell the range of white backgrounds (colour temperature 3400° K) within which a blue-green test flash (Ilford 603) is detected with rods and a red flash (Ilford 608) with cones. A 1 mm$^2$ pupil is assumed.

*The mesopic range.* There is for each ganglion cell a range of background illuminations (the mesopic range) within which long wave-length test flashes are detected through cones and short wave-length flashes through rods. In this range, the spectral sensitivity is changing from being that of rods to that of cones. For many experiments it is helpful to know through which receptor mechanism a light will be detected but that is not always

easy to specify, as the position and extent of the mesopic range (as defined above) vary with the wave-lengths of test and background lights. Experiments often involve white background lights, and estimates of a mesopic range for such backgrounds and test flashes of the colours used in the present experiments may be derived from increment–threshold curves like that of Fig. 2 by taking account of the scotopic and photopic effectiveness of the blue-green background light. This range is given graphically in Fig. 10, with background illumination expressed in units measured at the

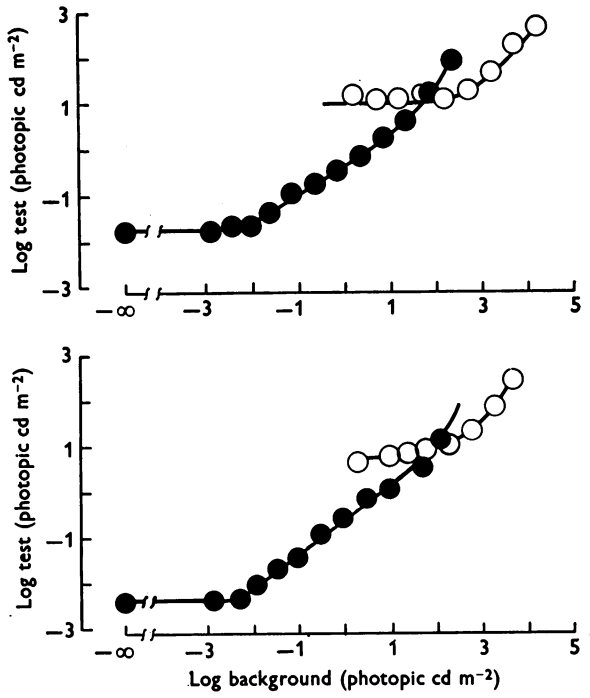


Fig. 11. Increment–threshold curves for two units, with ordinates and abscissae transformed to show the relative positions of rod and cone branches when the test and background lights are white (colour temperature 3400° K). Curves were made using a blue-green background light with, for the rod branch, a blue-green test (●) and, for the cone branch, a red test (○). A 1 mm² pupil is assumed. Upper unit 42/1, *X*-cell; lower unit 40/4, not identified as *X* or *Y*.

cornea for a white light of colour temperature 3400° K. If a 1 mm² pupil is assumed the middle of the mesopic range for most ganglion cells is about 20 cd m$^{-2}$. This estimate agrees with one given by Barlow & Levick (1968) but is lower by about a factor of 10 than those given by Daw & Pearlman (1969) and Hammond & James (1971). Since the latter workers

used a dilated pupil, the Stiles–Crawford effect may have contributed to the higher values they obtained.

By allowing for the scotopic and photopic densities of the coloured filters used in the measurement of increment thresholds, curves may be displayed as if they had been generated with tests and backgrounds that were white. This has been done in the graphs of Fig. 11 from which it appears that a threshold flash commonly would not be detected through cones until the rod system begins to saturate.

*Receptive field organization.* The spatial organization of receptive fields appears to be stable over the photopic range, for the balance of centre-surround antagonism revealed by area–threshold curves (Fig. 5) seemed unaltered by large changes in background illumination. This is not true in the scotopic range (Barlow *et al.* 1957). Detailed comparisons of scotopic and photopic receptive field organization in the same ganglion cell, and the interaction there of rod and cone signals, are the subjects of the following paper.

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