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CONVERGENCE OF ROD AND CONE SIGNALS IN THE CAT'S RETINA

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SUMMARY

1. In an attempt to understand the convergence of rod and cone signals in the cat's retina, ganglion cells that received inputs from both rods and cones were stimulated using lights chosen to excite one or other receptor system or both together.

2. If a mesopic background was chosen to allow the ganglion cell to be excited by a blue-green test flash primarily through rods and a deep red flash primarily through cones, one light could not be alternated with the other without eliciting a response from the cell.

3. This appears to be a result of the different temporal properties of the scotopic and photopic systems. On the mesopic background responses to blue-green test flashes were transient. Responses to red test flashes arose with similar latency, but were more sustained.

4. Rod and cone systems responded with similar latencies in the presence of the mesopic background that substantially light-adapted the rod system but left the full sensitivity of the cone system undiminished. When equivalently light-adapted, the cone system was faster.

5. When brief flashes that acted through rods were presented with flashes that acted through cones the ganglion cell's response was the sum of the responses to the two flashes presented separately, as long as the flashes were weak. This linear relation ceased to hold when flashes were strong, but the breakdown appears not to be the result of mutual inhibition between rod and cone signals.

6. When a background light excited both rod and cone systems it appeared to reduce sensitivity independently in each.

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7. The scotopic and photopic receptive fields of a given ganglion cell always were of the same type, on- or off-centre, and, within the limits of measurement, the central regions of the receptive fields were concentric and both the same size.

INTRODUCTION

The division of labour between rods and cones in the human eye is well known (e.g. Pirenne, 1967). Not only do the receptor systems subserve different functions, but even when stimulated together they often act independently. This is curious, in view of the multiplicity of contacts between rod and cone systems at different levels in the retina (Stell, 1972).

The cat retina would seem even less suited for independence of rod and cone systems, as it is less specialized for duplex function: it lacks a fovea, and although the distribution of cones is dense in the *area centralis*, that of rods is denser still. The mixing of rod and cone signals is seen in recordings from horizontal cells (Steinberg, 1969*a*, *b*, *c*) and from ganglion cells: units driven only by rods must be rare, although they have been described by Granit (1943) and by Andrews & Hammond (1970*a*). Thus rod and cone systems might be expected to behave more alike in cat than in man, and, when stimulated together, to be less independent.

The preceding paper showed that in many respects the cat's ganglion cells when driven by cones behave as they do when driven by rods. This paper extends these comparisons and describes also the behaviour of units when driven by rods and cones together.

METHODS

The experiments of this and the preceding paper (Enroth-Cugell, Hertz & Lennie, 1977) were made on the same ganglion cells, and the methods used were the same. As in the preceding paper, illuminations are expressed for rods as photons deg^{-2} sec^{-1} at 500 nm and for cones at 560 nm, equivalent to the light transmitted by the broadband filters used in the experiments.

RESULTS

Most comparisons of scotopic and photopic behaviour were made in the presence of a blue-green background chosen to be in the middle of the mesopic range. This made it possible to activate the rod system with a blue-green test flash and the cone system with a red one. Since the mesopic range varied from unit to unit (see Fig. 11 of preceding paper), it was necessary to establish the best background illumination by making, for each cell, increment–threshold curves for red and blue-green test flashes (Enroth-Cugell *et al.* 1977). Fig. 1 shows these for one unit. The background that best separated the rod and cone thresholds is marked by an arrow.

There, photopic (cone) threshold for detection of a red test flash was about 1·0 log unit lower than scotopic (rod) threshold, while for the blue-green flash the reverse was true. This degree of separation allowed considerable room for manoeuvre in the use of supra-threshold stimuli with negligible contribution from one mechanism to the response to a test flash intended for the other.

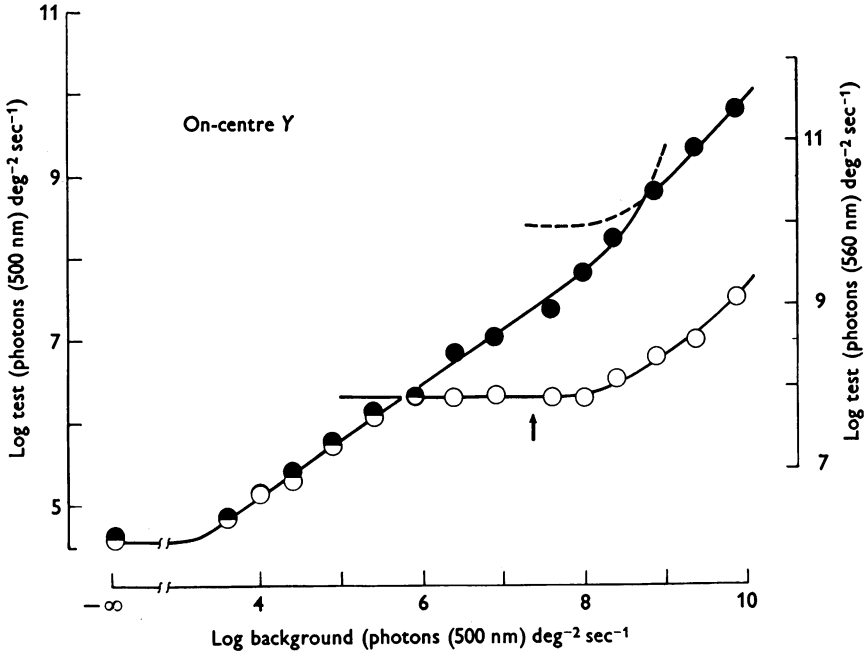

Fig. 1. Increment–threshold curves for red flashes (○) and blue-green flashes (●) delivered on a blue-green background. The background illumination that best separated the thresholds of the rod and cone systems to flashes of the two colours is marked by an arrow. The abscissa and left-hand ordinate give illuminations (at the cornea) in units appropriate for rods, while the right-hand ordinate, which applies only to the upper branch of the curve made with red flashes, gives illumination in units for cones. The line through the uppermost points obtained with blue-green flashes is the cone increment–threshold curve for red flashes, shifted vertically to predict the cone threshold for blue-green ones. Stimulus 4 Hz. Unit 39/4.

Temporal and intensive properties

A ganglion cell may be driven by its scotopic and photopic inputs together. The experiments described in the following sections were an attempt to compare the properties of the rod and cone signals when both can drive the ganglion cell, and to analyse the combination of these signals when they arise together.

The substitution of one light for a spectrally different one. This technique was introduced by Forbes, Burleigh & Neyland (1955) and developed for ganglion cells by Donner & Rushton (1959). It can be very useful in investigating the contributions of different receptor mechanisms to a single ganglion cell's discharge. If, as in these experiments, both the rod and the cone systems may contribute, then two lights of different spectral composition cannot (in general) be adjusted in illumination so that each receptor system catches the same number of photons from each light.

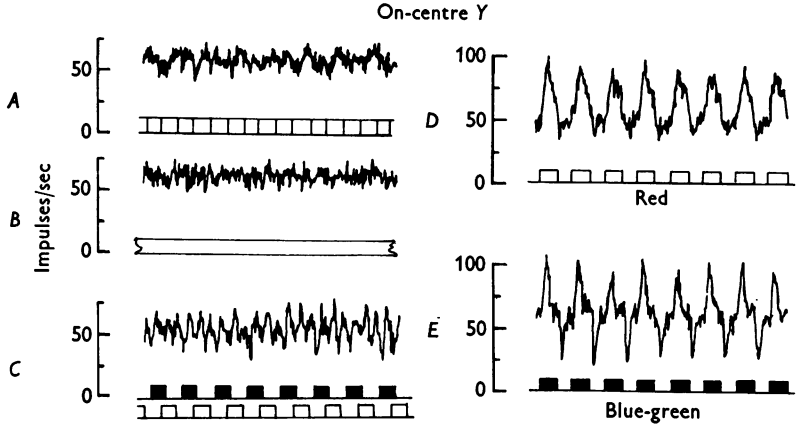

Fig. 2. Pulse-density tracings of responses to the alternation of test flashes. Stimulus diameter always 0·2 deg; flash duration and interflash interval 125 msec each. For all observations the blue-green background was fixed at 7·9 log photons (560 nm) deg^{-2} sec^{-1}. *A*, the response to the repeated substitution of one red flash for an identical one (9·3 log photons (560 nm) deg^{-2}sec^{-1}). *B*, the discharge in response to the steady presentation of a test spot of the illumination used in *A*. *C*, the quietest exchange of blue-green flashes and red ones (blue-green 9·0 log photons (500 nm) deg^{-2} sec^{-1}, red same as in *A* and *B*. Blue-green flashes led red ones by 143 deg. No adjustment of the illumination in the blue-green flash produced a weaker response. *D*, responses to repeated presentation of the red flash. *E*, responses to repeated presentation of the blue-green flash. Note the different time courses of responses in *D* and *E*. Unit 37/3.

Hence substitution of one light for the other will be signalled by at least one of the mechanisms. However, even if the two lights are equal for neither rods nor cones a silent substitution of one for the other can occur if special conditions are satisfied, namely that the signal at the offset of one is the inverse of the signal at the onset of the other, and the ganglion cell responds to their sum. Some experiments were made to see if these conditions could be met.

Test lights were chosen so that, when presented against the blue-green

background, the red one acted negligibly on the rod system and the blue-green one negligibly on the cone system (Fig. 1). Each test light, flashing on and off at 4 Hz, was carefully centred upon the middle of the receptive field, and its illumination adjusted to give a just-suprathreshold modulation of the maintained discharge. Then the two flashing lights were presented together, but 180 deg out of phase. We were unable to make a totally silent substitution as Rodieck & Rushton (1976) have reported, but with slight adjustments of the wedges in the test beams and the relative phases of the flickering lights, the transition from one light to another could be made barely audible. However, when we obtained records of these 'silent' alternations, it became clear that the substitution of one light for the other was incomplete, and unlike the truly silent substitution that could be obtained using two lights of the same colour.

The top left-hand record in Fig. 2 shows a pulse-density tracing of the response to the substitution of one red light for another; it is very similar to the tracing below it, which shows the average discharge to the red spot shone steadily upon the centre. The bottom left-hand record is the tracing of the quietest alternation of the red and blue-green lights. In that record there appears a spiky modulation of the discharge with a frequency three times that of the test light. This can be understood to reflect the rather better frequency response of the light-adapted rod system: the fundamental components of the scotopic and photopic responses are equal and in opposite phase, so for these components the alternation is truly silent, but there is insufficient third harmonic component in the photopic response to the square-wave stimulus to cancel that in the scotopic one. The two right-hand records show how different from each other were responses to these red and blue-green stimuli delivered separately. Responses to the blue-green flashes show a sharp discharge peak at light onset (with a corresponding dip after offset) that is lacking in responses to the red one. These differences in discharge pattern, which appear to be related to the different states of light adaptation of the rod and cone systems (see next section), probably account for our inability to find a silent exchange. Had we been able to stimulate together the rod and cone systems when equally light-adapted, or had we used stimuli containing only low temporal frequencies, a silent substitution might have been observed.

Time course and latency of discharge. In both the scotopic (Yoon, 1972; Enroth-Cugell & Shapley, 1973) and photopic (Enroth-Cugell *et al.* 1977) ranges the loss of sensitivity brought about by increasing background illumination is accompanied by a change in the time course of responses to flashes. Discharges become more transient as sensitivity is reduced,

so we expect that on a mesopic background, which substantially reduces the sensitivity of the rod system but may leave the cone system unadapted, the time courses of discharges to red and blue-green flashes would be different.

The responses shown in Fig. 3 were obtained using a background that had raised the scotopic threshold to about 3000 times its level in darkness and the photopic threshold to about 8 times its unadapted level (see inset).

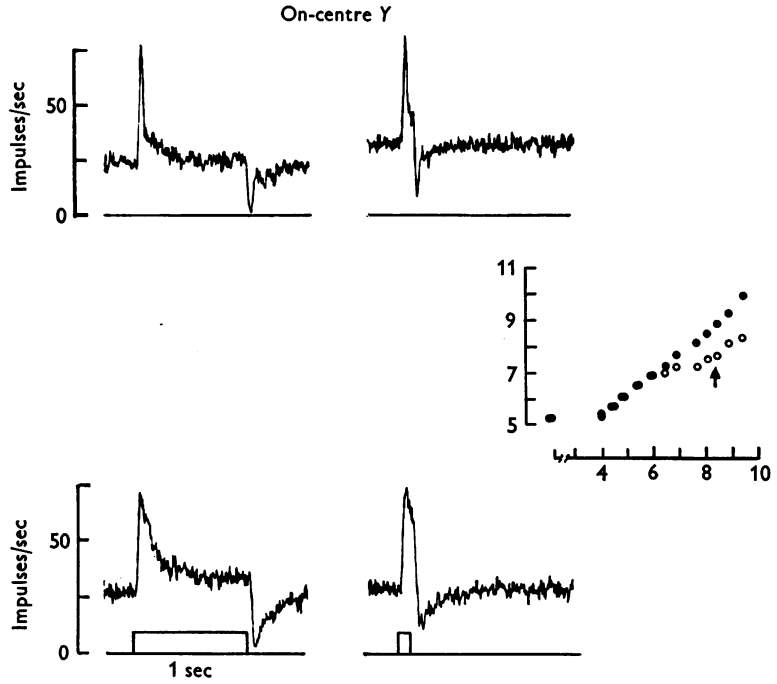

Fig. 3. Time course of responses to red and blue-green flashes on a mesopic background. Top row: responses to blue-green flashes of 1 sec (left) and 100 msec (right) duration. Bottom row: responses to red flashes of the same duration. Although all responses show almost the same peak discharge rate, those elicited by the blue-green flash are more transient than responses to the red flash. The inset shows the increment–threshold curves used in choosing the background for the experiment (arrowed). The ordinate and abscissa give, respectively, log test and background illuminations in photons (500 nm) deg^{-2} sec^{-1}. Same unit as in Fig. 2.

Stimuli were chosen so that peak discharge rates were almost the same, yet responses to blue-green tests (top) were much more transient than discharges to red tests (bottom).

Whenever experiments were made using mesopic backgrounds, responses to blue-green test flashes were predominantly transient and

responses to red flashes more sustained, as would be expected from differences in the levels of light adaptation. The sharper peaks and smaller sustained components in scotopic responses might be thought evidence for surround antagonism, but since each spot was carefully centred on the receptive field it is hard to see why one would activate the surround more than the other.

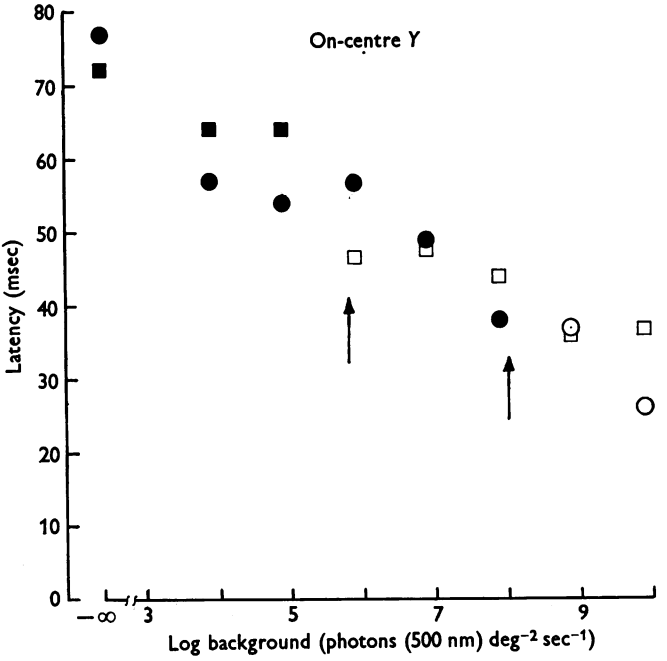

Fig. 4. Change in response latency with light adaptation. Points show latencies of weak responses to 50 msec test flashes that were red (squares) or blue-green (circles). Filled symbols indicate that the response was rod-driven, open symbols that it was cone-driven. There was no abrupt change in latency as one receptor system took over from the other. Arrows mark the mesopic range of background illuminations. Unit 42/2.

Although differences in time course of response to red and blue-green flashes may explain why a completely silent alternation of the stimuli could not be made in the experiment of Fig. 2, different latencies of response might also have contributed to that result.

Fig. 4 is based upon measurements made by the method described in the preceding paper (Enroth-Cugell *et al.* 1977) and shows the changes in latency of just-suprathreshold responses to red and blue-green test flashes as the blue-green background illumination was raised from complete darkness. Filled symbols indicate that the cell was driven by rods, open

symbols that it was driven by cones. Response latencies to both flashes became shorter with increasing background illumination, but there was no abrupt shortening of latency as the red flash became detectable through cones; on mesopic backgrounds (marked by arrows) responses of the rod and cone systems were equally fast. However, unadapted cone-driven responses clearly were faster than rod-driven ones obtained in the dark-adapted eye, and comparisons of latencies when rod and cone

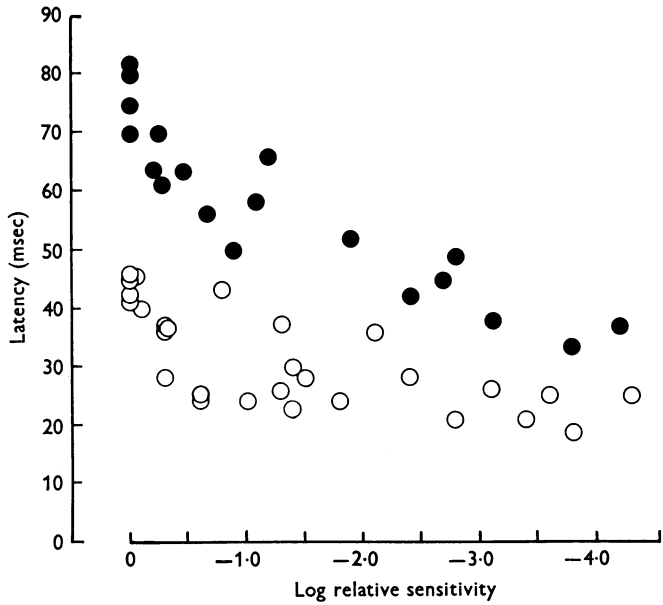

Fig. 5. Latencies for rod- and cone-driven responses as a function of adaptive state. All responses were of approximately the same magnitude and within the cell's linear response range. Latencies of cone-driven responses were obtained using red tests (○), those of rod-driven responses using blue-green tests (●). The abscissa gives sensitivity relative to its maximum unadapted value. At any one level of adaptation the cone system is faster, but the unadapted cone system and the light-adapted rod system have similar latencies. Results are from six X- and two Y-cells, and for all but two units both cone- and rod-driven responses are included.

systems were equally light-adapted (i.e. with thresholds equal multiples of the unadapted thresholds) shows that then the cone system was faster (Fig. 5).

Responses to brief flashes. Both when driven by rods (Barlow & Levick, 1969) and by cones (Enroth-Cugell *et al.* 1977) the ganglion cell's discharge of impulses is, over a limited range, proportional to the incremental

stimulus. Some experiments were made to establish whether, on mesopic backgrounds, the stimulus–response relationship outside the linear range is the same for the rod and cone systems.

The major difficulty in making comparisons upon the mesopic background results from the different temporal properties of the scotopic and photopic responses: different response measures can give different stimulus–response relationships. For flashes of light briefer than the integration time, the number of extra impulses discharged is a useful index of response,

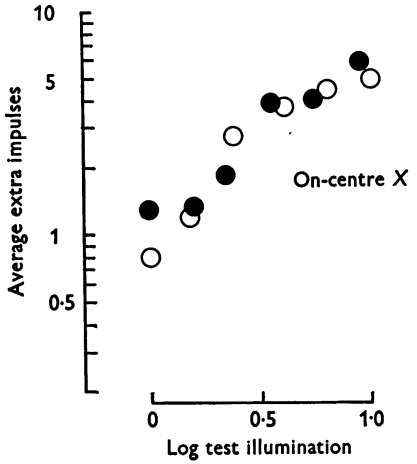

Fig. 6. Stimulus–response relations for rod and cone systems made using a blue-green background (6·8 log photons (560 nm) deg^{-2} sec^{-1}) that had left the cone system unadapted but had raised the threshold of the rod system 1·9 log units from its level in darkness. The average number of extra impulses discharged in 150 msec following onset of a blue-green (●) or red (○) test flash lasting 50 msec was measured from cumulative impulse counts of the kind described in the preceding paper (p. 310). Unit 40/4.

even though the distribution of these impulses in time often is not the same for the scotopic and photopic systems (Fig. 3). For the experiments described here extra impulses were counted in the 150 msec following flash onset, even though the biphasic character of scotopic responses (Fig. 3) in some cases slightly reduced the count. Impulse counts were taken from cumulative plots of the kind described on p. 310 of the preceding paper.

At mesopic background levels, where both may be stimulated, the rod and cone systems may not be equally sensitive. So, to free the comparison of stimulus–response characteristics from the difference in sensitivity, we plotted the number of extra impulses generated by a flash against the logarithm of stimulus illumination, with zero on the log scale representing the number of photons required to produce a criterion response in the

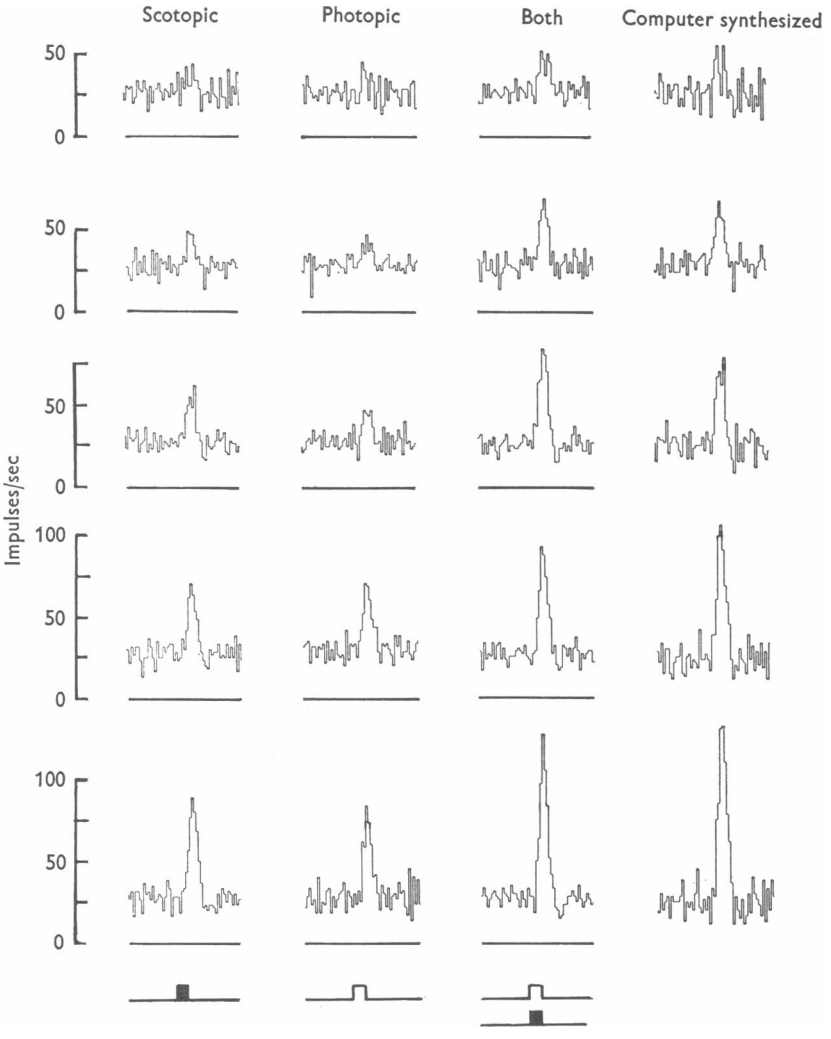

Fig. 7. The combination of responses to red and blue-green flashes 50 msec duration) presented simultaneously on a blue-green mesopic background. Rod-driven responses to blue-green flashes of progressively increased illuminations are shown in the left-hand column. In the next column are corresponding cone-driven responses to red flashes. The weakest blue-green flash delivered 6·6 log photons (500 nm) deg^{-2} sec^{-1} and the weakest red one 7·9 log photons (560 nm) deg^{-2} sec^{-1}. From top to bottom flash illumination was increased in 0·2 log unit steps. The third column shows the ganglion cell's responses to the two flashes presented together, and the fourth shows composite responses, synthesized in the computer, that are the sums of responses to the two flashes delivered separately (i.e. the sum of columns 1 and 2). Background illumination 7·8 log photons (500 nm) deg^{-2} sec^{-1}. Unit 43/1, not identified as *X* or *Y*.

linear range. This was done for five units (two *Y*-cells, one probably *X*, two not classified) and in every case the growth in discharge was similar for both mechanisms over the range where they could be isolated. Results from the (probable) *X*-cell are shown in Fig. 6.

Fig. 7 shows some results of an experiment to analyse the combination of responses to red and blue-green flashes presented simultaneously. The left-hand column of the figure shows histograms of responses to a blue-green flash of progressively increased illuminations; the column next to it displays responses to the corresponding red flash, and responses to the stimuli presented together are shown in the third column.

A simple way to test for the addition of scotopic and photopic responses is to compare the unit's response to the red and blue-green flashes presented simultaneously with a response synthesized by adding, in the computer, averaged responses to the two flashes presented separately. For each pair of flashes that contributed to the responses in column 3, a composite response synthesized from responses to the flashes delivered separately is presented on the right. When flashes were weak, synthesized responses were like real ones, but when the flashes were strong, synthesized responses were larger. This can be seen more clearly in Fig. 8, which displays the number of extra impulses discharged as the pairs of flashes increased in strength, against the number that would have resulted from perfect addition of responses to the flashes presented separately. This non-linearity must arise at or after the point of combination of rod and cone signals; the following analysis explores further the nature of their combination.

Stimulus–response relations determined for red and blue-green test flashes, delivered separately, are plotted in Fig. 9 as in Fig. 6. Then another set of measurements was made, this time with the flashes presented together. These measurements are shown as squares, and are drawn directly above the points that mark responses to the flashes presented separately. A continuous curve has been drawn by eye through the latter. This curve, scaled by a factor of 2 on the ordinate (dashed curve), would describe the responses to the pair of flashes presented together, if responses added perfectly, that is, if all the non-linearity shown by the stimulus–response curve arose before the point at which rod and cone signals are combined. Scaled by a factor of 2 on the abscissa, on the other hand, the same curve (now dot-dashed) would describe responses to the combined flashes if sensitivities added; i.e. if a red and a blue-green test flash, each of which produced a criterion response, when presented together produced the same criterion response when the illumination in each was halved. This would happen if all the non-linearity arose after the signals are combined (Levine & Abramov, 1975).

Over a limited range, the two predicted curves are very close, and our data could be said to agree with either one. At higher illuminations, however, the points for the combined test flashes lie below the line for addition of responses and to the left of their expected position on the line for summation of sensitivities. This means that even though the response to the combined stimulus is not as large as the sum of responses to individual stimuli, a combined rod and cone stimulus may be more effective than a rod stimulus alone or a cone stimulus alone. This finding is compatible with the existence of at least two compressive non-linearities (for example, power laws with exponent less than one), one occurring before the signals are combined and one at or after combination. Results like those were

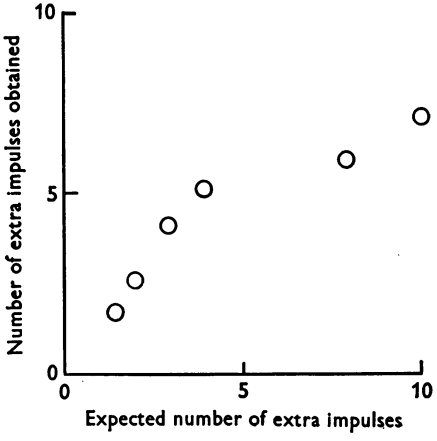

Fig. 8

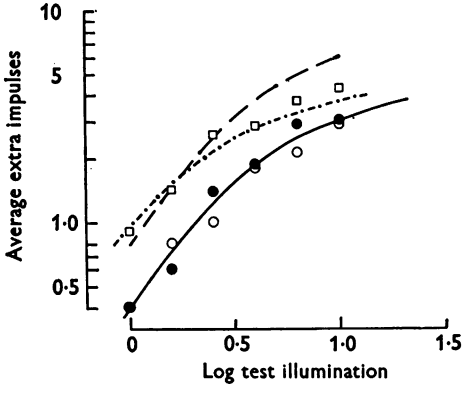

Fig. 9

Fig. 8. Combination of responses arising in rod and cone systems. The average number of extra impulses discharged in the 150 msec following the simultaneous presentation of a blue-green and a red flash is plotted against the number of extra impulses in the two responses to the flashes delivered separately. Except for the lowest point, impulse counts are from the same responses used in the construction of Fig. 7. Unit 43/1.

Fig. 9. Analysis of non-linearities in combination of responses to flashes. The average number of extra impulses discharged in response to a blue-green (●) or red (○) flash lasting 50 msec is plotted against the logarithm of flash illumination (relative to the illumination required for identical weak responses). Squares above each pair of points show the number of impulses discharged in response to the simultaneous presentation of the two flashes. The smooth line has been drawn to give the best fit (by eye) to the two sets of circles. When scaled by a factor of 2 on the ordinate (– – – –), this curve charts the expected position of the squares were the cell to add *responses*. Scaled by a factor of two on the abscissa (—·—·—), the line is the expected locus of the squares were the cell to add *sensitivities*. Background illumination 8·0 log photons (500 mm) deg^{-2} sec^{-1}. Unit 43/3, not identified as *X* or *Y*.

obtained in experiments on four other cells (the unit of Fig. 6, two *Y*-cells, and one not identified as *X* or *Y*). Our results do not rule out the possibility that rod and cone signals interfere with each other, but if they do inhibit each other the interference is not strong enough in our experiments for one type of signal to block the other completely.

In experiments made upon monkey ganglion cells, Gouras & Link (1966) observed an occlusive interaction of rod and cone signals when the two test flashes were separated by a critical interval. This interval was of the order of 50 msec, enough to compensate for the longer latency of their scotopic responses. But we have just seen that cone and rod signals arrive at the cat's ganglion cells with similar latencies when mesopic backgrounds are used (Fig. 4), so the experiments of Figs. 7–9 provided conditions quite favourable for interactions. However, to explore the matter further, some experiments were made with flashes presented asynchronously.

Red and blue-green test flashes were chosen to produce small photopic and scotopic responses of approximately equal magnitude. The flashes were then presented together or separated by a delay, which varied in steps of 20 msec, of up to 140 msec. This was done both with the red flash leading and the blue-green one leading. Composite averaged responses to the coupled pair of flashes were synthesized in the computer from the response to each presented alone, and in Fig. 10 these are arranged on the right-hand side for comparison with the ganglion cell's responses, shown on the left. At the top of the Figure are tracings of responses to the two flashes presented separately.

Over the whole range of inter-flash intervals the ganglion cell's discharge was almost indistinguishable from the computer's synthesis of it, a result seen in experiments on four additional cells (one *X*-cell, two *Y*-cells and one not identified as *X* or *Y*).

Independent action of backgrounds. A blue-green mesopic background was used in the preceding experiments because its scotopic luminance was greater than its photopic luminance. Fig. 1 shows that over a large range this background had no effect upon photopic sensitivity. When the background did alter photopic sensitivity it must have done so through cones because the rod system was by then saturated.

Some measurements were made to establish whether scotopic sensitivity depended upon a background's effect on cones. From three units increment–threshold curves were obtained with a blue-green test flash presented first against a blue-green background and then against a red one. When scotopically equal to the blue-green one, the red background was 1·85 log units stronger for cones. Some results from one unit are given in Fig. 11. Were the sensitivity of the scotopic system influenced

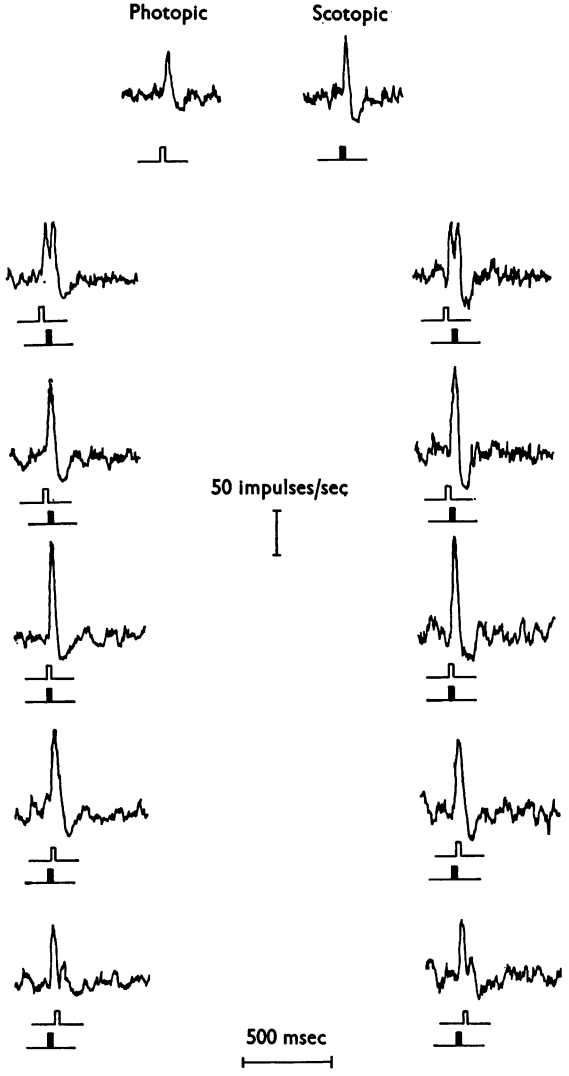

Fig. 10. Combination of responses to asynchronous red and blue-green flashes. The top two traces show pulse–density tracings of responses to the two 50 msec flashes delivered separately. Open stimulus markers denote red flashes, filled ones denote blue-green flashes. Underneath in the left-hand column are the ganglion cell's responses to the combined stimuli delivered with various onset asynchronies. The right-hand column shows composite responses to the two flashes, synthesized in the computer by adding individual responses with the appropriate delays. Real and synthesized responses are virtually indistinguishable. With the red flash leading, onset asynchronies are, from top to bottom, 80, 40, 0, −40, −80 msec. Blue-green background 8·0 log photons (500 nm) $deg^{-2}\,sec^{-1}$. Same unit as in Fig. 9.

only by the effect of the background upon rods, the two curves would coincide, for both the red and blue-green backgrounds are expressed in equivalent photons at 500 nm. The curves do not coincide exactly but the discrepancy is within the range of experimental error. One other unit provided results like those from Fig. 11. The curves from the third unit coincided exactly. These results are in good agreement with similar ones obtained by Daw & Pearlman (1971) in experiments to measure the spectral sensitivity to background lights that saturated the rod system.

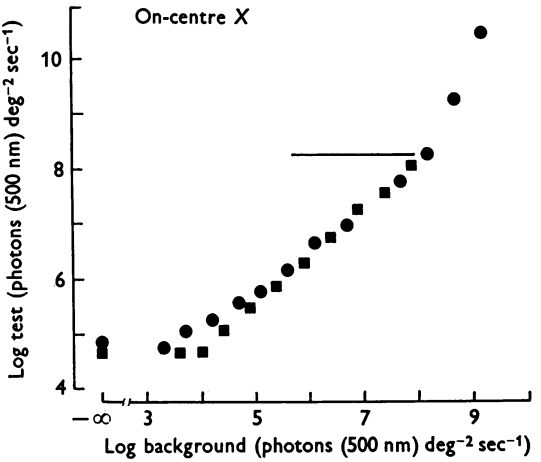

Fig. 11. Scotopic increment–threshold curves for a blue-green test flash (4 Hz flicker, 0·2 deg diameter) presented upon a blue-green (■) or red (●) background. The horizontal bar marks the photopic threshold for the flash when the background was blue-green. Unit 45/3, *X*-cell.

Spatial properties

Spatial summation for test lights. In a graph where the illumination required for detection of a test flash is plotted against test size, commonly threshold first falls with increases in spot size, and later rises, before it becomes independent of spot area. The curve is taken to reflect the pooling of receptor signals from the central and peripheral regions of the receptive field.

It should be possible to compare the spatial properties of scotopic and photopic receptive fields by making area–threshold curves for red and blue-green test flashes presented against the mesopic background. Such curves, made from the threshold responses of one unit, are given in Fig. 12 together with two further curves that are based on responses from the unit when fully dark-adapted (bottom) and very light-adapted (top). In the lowest graph, the points are well fitted by a line of slope −2 (Ricco's law)

for test spots up to about 2° in diameter. Further increases in spot size had no influence on threshold. This region of perfect summation was similar at all background levels, and its extent may be characterized by the intersection of the sloping line and a horizontal line drawn through the lowest points on the curve (the diameter, D_t, of the 'central summing area'; Cleland & Enroth-Cugell, 1968). Fig. 13 gives D_t for the photopic receptive field against D_t for the scotopic one, for the units on which measurements were made. There was no systematic difference between the two.

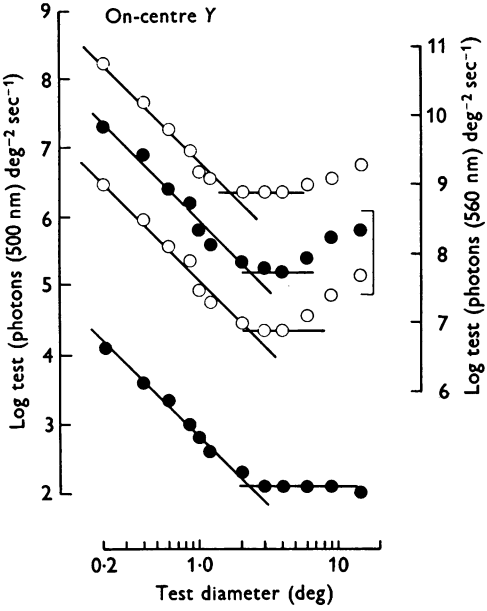

Fig. 12. Area–threshold curves for blue-green flashes (●) and red flashes (○) at different background illuminations. The lowest curve was made in the fully dark-adapted eye. The middle two curves were made using the same blue-green mesopic background (equivalent to 7·4 log photons (500 nm), 6·9 log photons (560 nm) deg^{-2} sec^{-1}), but are separated on the ordinate because the red test flash acted through cones and the blue-green one through rods. The uppermost curve was made using the highest blue-green background illumination attainable (9·4 log photons (560 nm) deg^{-2} sec^{-1}). For clarity, this curve has been shifted up 1·25 log units from its correct position on the ordinate. The right-hand ordinate is appropriate only for the photopic thresholds measured with red flashes. Flash duration 50 msec. Unit 39/4.

When the unit of Fig. 12 was dark-adapted, its surround was relatively insensitive, and test spots that extended beyond the region of summation caused no rise in threshold. At higher background levels the surround

was activated by large test spots, but, like Barlow, Fitzhugh & Kuffler (1957), we obtained no evidence, from this or from other units, to suggest that it becomes more active following the transition from scotopic to photopic thresholds. The surround contribution thus appears to be constant at all but the lowest backgrounds (Enroth-Cugell & Lennie, 1975).

Within the limits of measurement, scotopic and photopic receptive fields of all units were concentric.

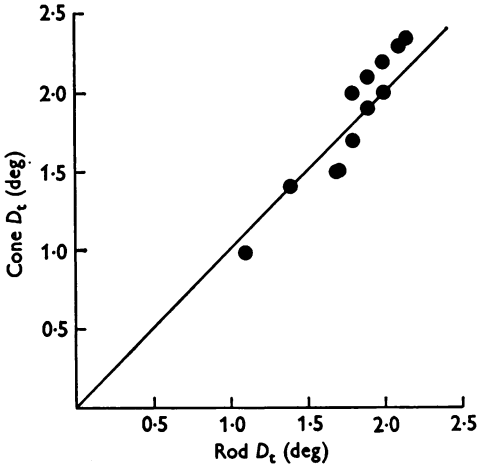

Fig. 13. Comparison of scotopic and photopic central summing areas of eleven units. D_t for the cone system is plotted against D_t for the rod system. There was no systematic difference between the two.

Spatial summation for adapting lights. It was shown for the scotopic system by Cleland & Enroth-Cugell (1968), and for the photopic system in the preceding paper, that the central area over which a ganglion cell pools the effects of steady adapting lights matches its area for summation of signals from test lights. Since the latter areas are the same in the scotopic and photopic systems (Fig. 13), it follows that the areas for summation of adapting lights should be also. Comparisons could not be made with the usual mesopic background, because that rarely had any effect upon photopic sensitivity. Instead, conditions were arranged so that, first, scotopic threshold for a small blue-green test flash was kept constant about 3·0 log units above its minimum, by adjustments of background illumination as background size was varied. Then we found, for each background size, the illumination needed to keep photopic threshold for a red test flash constant at about 1·0 log unit above its lowest level. Such area–threshold curves show the extent of pooling of adaptive signals in the

rod and cone systems. For one unit these curves are compared in Fig. 14. Adaptive signals from backgrounds seem to be accumulated over a region that is substantially the same for rod and cone systems.

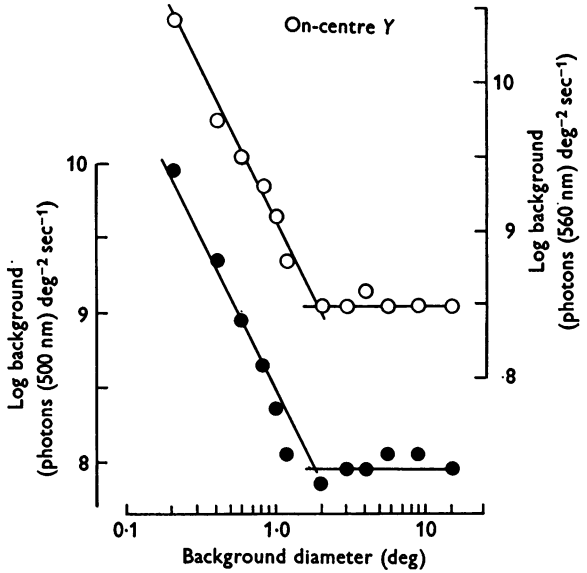

Fig. 14. Spatial summation of adapting lights in the rod and cone systems. For the rod system a blue-green test flash (4 Hz flicker) was kept at threshold 3·0 log units above the minimum threshold by adjustment of background illumination as background size was varied. The resulting curve of adaptive sensitivity is shown by filled circles. The adaptive sensitivity of the cone system, measured in the same way but with cone threshold kept 1 log unit above its minimum, is shown by open circles. Areas of summation are not distinguishably different. Unit 42/2.

DISCUSSION

The measurements described here suggest the following principles.

(*a*) At mesopic background levels rod and cone signals arrive at the ganglion cell with similar latencies. The cell responds to the sum of the signals, but only for threshold or slightly suprathreshold flashes does the response vary linearly with illumination.

(*b*) A background light affects scotopic and photopic sensitivities independently.

(*c*) Scotopic and photopic receptive fields are concentric, are of the same type (on- or off-centre) and have similar spatial properties.

Several of these properties fit well with established findings, but some are hard to reconcile with other physiological observations.

The combination of rod and cone signals from test flashes. When flashes were presented upon a mesopic background, scotopic and photopic responses were equally fast (Fig. 4) and were distinguished not by their latencies but by their time courses (Fig. 3). The unadapted photopic response of a ganglion cell is faster than the dark-adapted scotopic one by up to 30 msec but mesopic backgrounds that light-adapt the rod system reduce the latency of its response (Fig. 4). When both systems are un-adapted, the difference between their response latencies is similar to that found in the monkey (Gouras & Link, 1966).

Andrews & Hammond (1970*b*) attempted to differentiate rod and cone contributions to responses by assuming that the early and late phases of the discharge in response to an intense, prolonged stimulus reflected, respectively, cone and rod signals. They reported that, when stimuli were presented against a mesopic background, the photopic component of response was fast and transient, the scotopic one slow and sustained. The isolation of rod and cone systems was not verified independently, which is unfortunate, for the form of response observed, an initial transient discharge ('P1') decaying rapidly, sometimes followed by an overshoot, to a steadier level ('P2') may be obtained from the rod system alone. It is especially easy to evoke if the stimulus is relatively large, for then surround antagonism is aroused, which clips off more sharply an already transient on-discharge (e.g. Rodieck & Stone, 1965). In our experiments transient cone-driven responses were seen at high levels of adaptation (Fig. 6, preceding paper) but these were never as transient as rod-driven responses obtained at comparable levels of light adaptation.

Within the range of stimulus strengths used in our experiments, the ganglion cell responds to the sum of the rod and cone signals that reach it, whether or not they arrive together. It has been observed in the monkey that whichever of the rod or cone signals arrives first causes some temporary refractoriness to the other (Gouras & Link, 1966). It is instructive to explore the differences in experimental conditions, for these probably are sufficient to account for the discrepant results. Two features of the experiments on monkey are important: the low maintained discharge and the use of diffuse flashes as test stimuli.

Absence of a maintained discharge would make undetectable any transitory suppression of responsiveness that may occur following a stimulus flash. This can be seen in Fig. 10, which shows responses to pairs of flashes with a variable interval between them. The effect of cone signals arriving at the ganglion cell during the post-discharge dip in the scotopic response was virtually lost in that dip, even though there was no suppression of cone signals by rod ones; they were simply added together. But without the maintained discharge as a platform against which increases

and decreases in signal could be registered, it might have been concluded that the rod signals inhibited those from cones. In the cat, the post-discharge dip following a weak stimulus is seen only in the light-adapted eye, but when strong stimuli are used, dips appear also in the dark-adapted eye, and the same might be expected of the monkey.

Gouras & Link used diffuse flashes that probably elicited surround antagonism. The complicated interplay of excitation and inhibition between centre and surround, taking place at different times on the scotopic and photopic systems is not easy to predict and could be an additional factor that contributes to the apparent interference between rod and cone signals.

It is difficult to compare our findings with the psychophysical ones but an experiment which does resemble ours provided results consistent with them. MacLeod (1972) found that when rod and cone systems each were excited by a suprathreshold flickering light, the resulting visual sensation was that expected from the additive combination of signals from rods and cones.

The influence of backgrounds. Increment–threshold curves like the one of Fig. 1 show that, over a substantial range, backgrounds that affect scotopic threshold do not influence the photopic one. The experiments of Fig. 11, in which increment–threshold curves were made using different coloured backgrounds, suggest that cone signals do not affect the scotopic threshold.

Horizontal cells have been implicated in the mechanism by which backgrounds control sensitivity (Enroth-Cugell & Shapley, 1973; Werblin, 1974), and since rod and cone signals appear together in S-potentials recorded from the cat's horizontal cells (Steinberg, 1969*a*, *b*, *c*; Niemeyer & Gouras, 1973) it seems curious that lights act so independently on the two systems. The paradox becomes less troublesome when account is taken of the conditions under which the various results are obtained.

From increment–threshold curves it is seen that diffuse background lights usually have begun to saturate the scotopic system at levels where they can alter a ganglion cell's photopic sensitivity. Thus, although the rod component in the S-potential could be involved in the control of photopic sensitivity, it would often be saturated and its effect would no longer vary with background illumination.

The observations made on the cat's ganglion cells agree well with those made psychophysically on man. Stiles' measurements (1939; Flamant & Stiles, 1948) show that rod threshold for a test flash is influenced by a background according to the background's scotopic luminosity, although a small break-down of this relation at higher background levels has been found by Makous & Boothe (1974) who show that red backgrounds raise

scotopic threshold a little more effectively than scotopically equal blue ones.

The surprising thing about rod-cone convergence in the cat's retina is how independently the two systems act when stimulated together.

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REFERENCES

ANDREWS, D. P. & HAMMOND, P. (1970*a*). Mesopic increment threshold spectral sensitivity of single optic tract fibres in the cat: cone-rod interaction. *J. Physiol.* **209**, 65–81.

ANDREWS, D. P. & HAMMOND, P. (1970*b*). Suprathreshold spectral properties of single optic tract fibres in cat, under mesopic adaptation: cone-rod interaction. *J. Physiol.* **209**, 83–103.

BARLOW, H. B., FITZHUGH, R. & KUFFLER, S. W. (1957). Change of organization in the receptive fields of the cat's retina during dark adaptation. *J. Physiol.* **137**, 338–354.

BARLOW, H. B. & LEVICK, W. R. (1969). Three factors limiting the reliable detection of light by retinal ganglion cells of the cat. *J. Physiol.* **200**, 1–24.

CLELAND, B. G. & ENROTH-CUGELL, C. (1968). Quantitative aspects of sensitivity and summation in the cat retina. *J. Physiol.* **198**, 17–38.

DAW, N. W. & PEARLMAN, A. L. (1971). Rod saturation in the cat. *Vision Res.* **11**, 1361–1364.

DONNER, K. O. & RUSHTON, W. A. H. (1959). Retinal stimulation by light substitution. *J. Physiol.* **149**, 288–302.

ENROTH-CUGELL, C., HERTZ, B. G. & LENNIE, P. (1977). Cone signals in the cat's retina. *J. Physiol.* **269**, 273–296.

ENROTH-CUGELL, C. & LENNIE, P. (1975). The control of retinal ganglion cell discharge by receptive field surrounds. *J. Physiol.* **247**, 551–578.

ENROTH-CUGELL, C. & SHAPLEY, R. M. (1973). Adaptation and dynamics of cat retinal ganglion cells. *J. Physiol.* **233**, 271-310.

FLAMANT, F. & STILES, W. S. (1948). The directional and spectral sensitivities of the retinal rods to adapting fields of different wavelengths. *J. Physiol.* **107**, 187-202.

FORBES, A., BURLEIGH, S. & NEYLAND, M. (1955). Electric responses to color shift in frog and turtle retina. *J. Neurophysiol.* **18**, 517–535.

GOURAS, P. & LINK, K. (1966). Rod and cone interaction in dark-adapted monkey ganglion cells. *J. Physiol.* **184**, 499–510.

GRANIT, R. (1943). The spectral properties of the visual receptors of the cat. *Acta physiol. scand.* **5**, 219–229.

LEVINE, M. W. & ABRAMOV, I. (1975). An analysis of spatial summation in the receptive fields of goldfish retinal ganglion cells. *Vision Res.* **15**, 777–789.

MACLEOD, D. I. A. (1972). Rods cancel cones in flicker. *Nature, Lond.* **235**, 173–174.

MAKOUS, W. & BOOTHE, R. (1974). Cones block signals from rods. *Vision Res.* **14**, 285–294.

NIEMEYER, G. & GOURAS, P. (1973). Rod and cone signals in S-potentials of the isolated perfused eye. *Vision Res.* **13**, 1603–1612.

PIRENNE, M. H. (1967). *Vision and the Eye*, chap. 3. London: Science Paperbacks and Chapman and Hall, Ltd.

RODIECK, R. W. & RUSHTON, W. A. H. (1976). Cancellation of rod signals by cones, and cone signals by rods in the cat retina. *J. Physiol.* **254**, 775–785.

RODIECK, R. W. & STONE, J. (1965). Analysis of receptive fields of cat retinal ganglion cells. *J. Neurophysiol.* **28**, 833–849.

STEINBERG, R. H. (1969*a*). Rod and cone contributions to S-potentials from the cat retina. *Vision Res.* **9**, 1319–1329.

STEINBERG, R. H. (1969*b*). Rod-cone interaction in S-potentials from the cat retina. *Vision Res.* **9**, 1331–1344.

STEINBERG, R. H. (1969*c*). The rod after-effect in S-potentials from the cat retina. *Vision Res.* **9**, 1345–1356.

STELL, W. K. (1972). The morphological organization of the vertebrate retina. In *Handbook of Sensory Physiology*, vol. VII/2: Physiology of Photoreceptor Organs, ed. FUORTES, M. G. F. New York: Springer-Verlag.

STILES, W. S. (1939). The directional sensitivity of the retina and the spectral sensitivities of the rods and cones. *Proc. R. Soc.* B **127**, 64–105.

WERBLIN, F. S. (1974). Control of retinal sensitivity. II. Lateral interactions at the outer plexiform layer. *J. gen. Physiol.* **63**, 62–87.

YOON, M. (1972). Influence of adaptation level on response pattern and sensitivity of ganglion cells in the cat's retina. *J. Physiol.* **221**, 93–104.