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THE EFFECTS OF REMOTE RETINAL STIMULATION ON THE RESPONSES OF CAT RETINAL GANGLION CELLS

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SUMMARY

1. Action potentials were recorded from optic nerve fibres of lightly anaesthetized cats while parts of the retina remote from the receptive field were stimulated by a shifting grating.

2. Vigorous responses can be obtained under these conditions, confirming McIlwain (1966), Krüger & Fischer (1973), and others.

3. These 'shift responses' are not caused by fluctuations of stray light because (*a*) they cannot be reduced by deliberately increasing or decreasing the light falling on the receptive field synchronously with the shifting grating; (*b*) a steady adapting light applied to the receptive field does not raise the threshold for the responses, whereas adapting light on the peripheral retina does, and (*c*) the threshold for the responses is elevated more following bleaching adaptation of the periphery than following bleaching adaptation of the centre.

4. Shift responses are strong, of short latency, and brief in duration in brisk-transient (Y-type) neurones. With few exceptions they are weak but long-lasting in brisk-sustained (X-type) neurones.

5. Shift responses are unlike responses from the main receptive field in having a distinct threshold; the magnitude of the response to weak gratings is not simply proportional to contrast, as is the case with weak stimuli applied to the receptive field.

6. It is thought that the excitatory pathway may involve amacrine cells, and that this mechanism may be concerned with the detection of the shifts of the image that occur with saccadic eye movements.

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INTRODUCTION

Hartline (1940) introduced the concept of a spatially limited receptive field and it came to be accepted that retinal ganglion cells could only be influenced by the light-induced activity of receptors lying within a strictly limited part of the retina (Kuffler, 1953). However McIlwain (1964) showed that stimulation of remote regions of retina could cause a slow increase of the maintained discharge, and could also increase the responsiveness of a ganglion cell to stimulation by a localized test spot of light, and he later (McIlwain, 1966) showed that the sudden movement of contours well outside the normal receptive field led to a discharge of latency below 100 msec. These effects have been confirmed and the distinction between the short-latency *modulated periphery effect* and the slowly waxing and waning *unmodulated periphery effect* has been further analysed by Ikeda & Wright (1972). These authors and Cleland, Dubin & Levick (1971) agree that periphery effects are prominent in brisk-transient, Y-type ganglion cells, but weak or absent in the brisk-sustained, X-type. Indeed the presence of the periphery effect is one of the battery of tests employed by the latter authors to distinguish the two classes of cells, and in a later paper (Cleland, Levick & Sanderson, 1973) they describe another test which probably involves the same retinal property, namely responsiveness to rotation of a radial grating centred on the receptive field.

With the exception of this last observation, which the authors attributed to stimulation of the classical receptive field surround, all the responses so far attributed to the periphery effect were small in relation to the maximum discharge frequency that a ganglion cell can produce. However Krüger & Fischer (1973) showed discharges, elicited by stimulation of retina at least 20° away from the centre of the receptive field, that rose to 200 impulses/sec or more. To produce these very vigorous responses they suddenly shifted by one half-period a grating covering almost the whole visual field except for a large region centred on the receptive field. In a later paper (Fischer, Krüger & Droll, 1975) they measured the effect of the grating contrast and of its amplitude and velocity of movement.

Although the slow, unmodulated, periphery effect has been shown not to be due to stray light or other artifacts (Levick, Oyster & Davis, 1965), the demonstration by Krüger & Fischer (1973) of crisp, short-latency responses as vigorous as those elicited from the receptive field centre made us suspicious of possible contamination by scattered light. We therefore did the experiments to be described here which, we think, vindicate Krüger & Fischer and show conclusively that a neural mechanism with some surprising properties gives rise to the shift effect; stray light is not an important factor.

METHODS

Preparation

Adult cats were anaesthetized initially with Halothane and during surgery were kept anaesthetized with methohexitone sodium (Brietal) given intravenously. The cervical sympathetic trunk was cut bilaterally and the trachea cannulated before the cat was set up in the stereotaxic apparatus. Then a circular piece of bone was removed from the skull above the optic tract just anterior to the lateral geniculate nucleus. After surgery the cat was kept lightly anaesthetized and paralysed with a continuous infusion of urethane (50 mg/kg.hr following an initial dose of 200 mg/kg) and gallamine triethiodide (Flaxedil: 10 mg/kg.hr).

The corneae were protected with contact lenses of zero power during preparation and recording, and the pupils fully dilated with atropine or homatropine. Phenylephrine hydrochloride was used to retract the nictitating membrane. Sometimes 3 mm artificial pupils on the contact lenses were used and residual refractive errors corrected with supplementary ophthalmic lenses, but as both of these procedures can introduce spurious effects when wide fields of view are necessary, they were often omitted. Accurate focusing is not a critical matter in these experiments, for we are concerned with light scattered to remote regions of the retina rather than refractive errors that cause blurring only over small retinal distances.

Data collection and analysis

The discharges of single optic tract fibres were recorded with a tungsten-in-glass micro-electrode. Action potentials were shaped to standard pulses that were accumulated by a PDP 11 computer which prepared PSTHs (peri-stimulus-time-histograms) and wrote them out on an $X-Y$ plotter. The computer also controlled the delivery of stimuli (see below).

Visual stimuli

These were projected from both front and rear on to a thin paper screen supported by Perspex set tangentially at a distance of 57 cm from the cat's eyes. Usually shift effects were generated by a grating of period 0·18 cycles/deg projected from the rear after reflexion from a galvanometer mirror that enabled the image to be moved quickly a known distance. Luminance was controlled by crossed polaroids and also by varying the projector voltage. The total width of the screen was 120 cm, and it could be positioned so that receptive fields within the central 50° of vision could be centrally located on the screen. Opaque cardboard disks were placed on the front of the screen to occlude partially the view of the grating; we usually employed a 30 cm disk centred on the receptive field. On the front of the paper screen or occluding disk two projectors focused spots or annuli; these were controlled in luminance by crossed polaroids and by varying the projector voltages. A penmotor-driven shutter controlled by the computer could occlude one or both of the beams. In addition a small amount of ambient room light fell on both sides of the screen.

Luminances were measured with an SEI visual photometer or a modified Tektronix-J 16 photometer, standardized by a calibrated 'Betalight' (Saunders Roe Developments).

Classification of receptive fields

Different classes of units were discriminated by several tests. Sinusoidal grating patterns made on an oscilloscope were exchanged for uniform fields of the same mean luminance (about 200 cd/m^2) in an attempt to find a grating position that

allowed a silent exchange. Tests were also made with gratings drifting slowly across the receptive field: in these cases we looked for changes in the mean rate of discharge as spatial frequency was altered (Enroth-Cugell & Robson, 1966). Qualitative observations were made of optimum stimulus size, and of responses to sustained contrast, rapid movement of a spot, and on–off changes in overall illumination. Using this battery of tests we rarely had any difficulty in deciding whether a cell belonged to the X or Y class of Enroth-Cugell & Robson. These correspond to the brisk-sustained and brisk-transient classes of Cleland & Levick (1974), and no certain members of their other classes were found.

RESULTS

Fig. 1 shows response histograms of Y-type (left) and X-type (right) cells to shifts of the grating in the stimulus configuration shown at bottom right. In both cases the receptive fields were centred in the 30 degree zone where the view of the grating was obscured. The grating was suddenly shifted when the marker traces move downwards and was returned when they move upwards, a complete cycle occupying 1 sec for the top traces. Responses were averaged over 30 cycles, and the numbers of impulses per 10 msec bin have been converted to discharge rates in impulse/sec. The Y-type cell (trace *A*) shows a brisk response with a latency under 100 msec for each phase of the movement. No response is visible for the X-type cell (trace *D*), but the discharge rate was actually elevated compared with the maintained discharge recorded during a period when the grating was not being shifted to and fro, which is shown in trace *E*. If the repeat cycle was slowed to 10 sec it became clear that this X-cell showed a response to each shift and return of the grating (*F* and *G*) but it was small and sluggish compared with the responses of the Y-cell at these slow rates (*B* and *C*). Note that *B*, *C*, *F* and *G* show only 800 msec following each shift, the bin width being 10 msec as in *A*, *D* and *E*.

Though the responses shown in Fig. 1 are typical of both X- and Y-type cells, we have occasionally recorded cells that were classified as brisk-sustained, X-type, by the usual test, yet gave a much more vigorous shift effect than that shown in Fig. 1*D*, *F* and *G*. Noda (1975) reported as many as 25% of units from the optic tract that showed 'mixed' properties, as judged from the responses to saccades in awake cats.

The pronounced difference between X- and Y-type cells does not support the notion that responses to shifting gratings are caused by scattered light, but we proceed to the following experiments in order to exclude it. There should be no change in the total flux entering the eye when the grating moves, but this may not be exactly true, and even when it is, inhomogeneities of retinal reflexion or of the media could cause the scattered light reaching the receptive field to be different for the two positions of the grating, thus possibly generating the response from the classical receptive

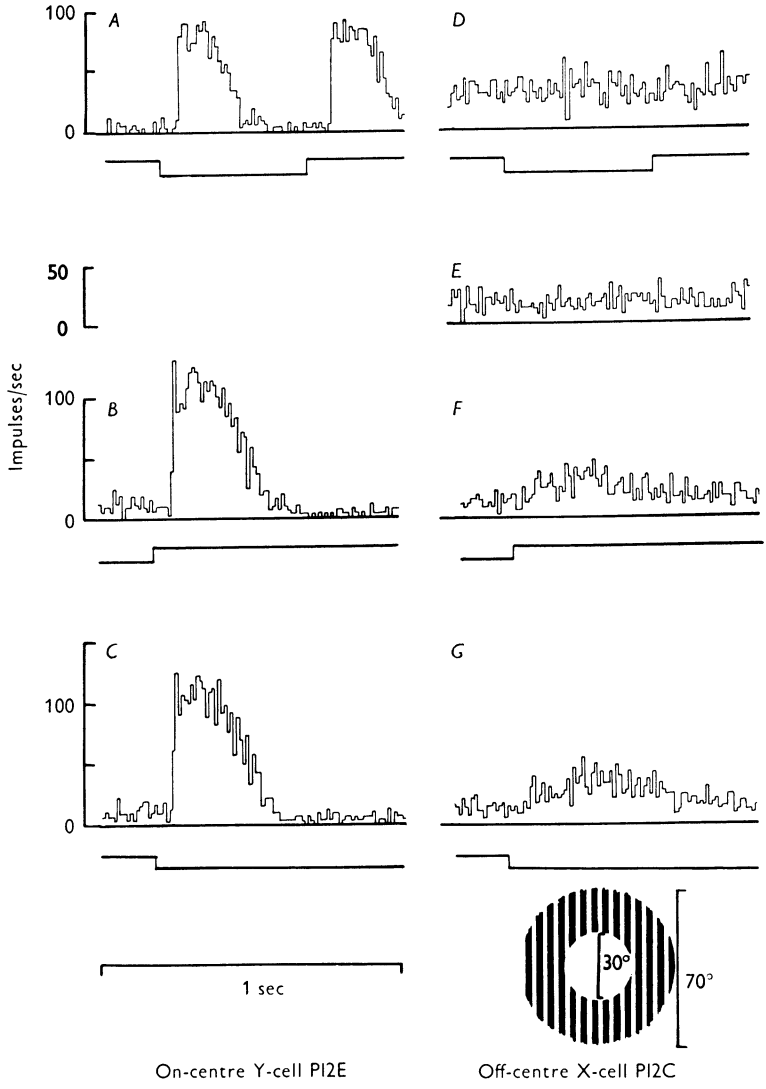


Fig. 1. Responses of a typical Y-cell (traces *A–C*) and X-cell (traces *D–G*) to a shift of the grating shown at bottom right. The receptive fields were centred in the central 30° disk where the view of the grating was occluded. For *A* and *D* the repeat cycle was 1 sec; no response is visible for the X-cell in *D*, though the maintained discharge is elevated in comparison with *E*, where the grating did not move. For *B*, *C*, *F* and *G* the repeat cycle was slowed to 10 sec, and this reveals the rather sluggish response of the X-cell. The bright bars of the grating had luminance 1·5 cd/m², the dark bars 0·5 cd/m², and the occluding disk 0·2 cd/m². In this and all other records the impulse densities are given as impulses/sec. The bin width was 10 msec, and there were thirty repeats; hence 30 impulses/bin is equivalent to 100 impulses/sec.

field. To ensure that total flux stayed the same we took care that the total number of bright bars visible from the cat's position was the same for the two grating positions, and also that there were no specular reflexions or other oddities that could lead to changes of flux; nothing of this sort could be observed from the cat's position. To improve the symmetry we also used rotating radial gratings, obtaining very similar results. Furthermore in a situation such as that in Fig. 1 it is quite simple to show that the response is not elicited from any particular part of the peripheral retina; obscuring the cat's view of various parts of the shifting grating reduces the response slightly, but no single region is essential or especially effective.

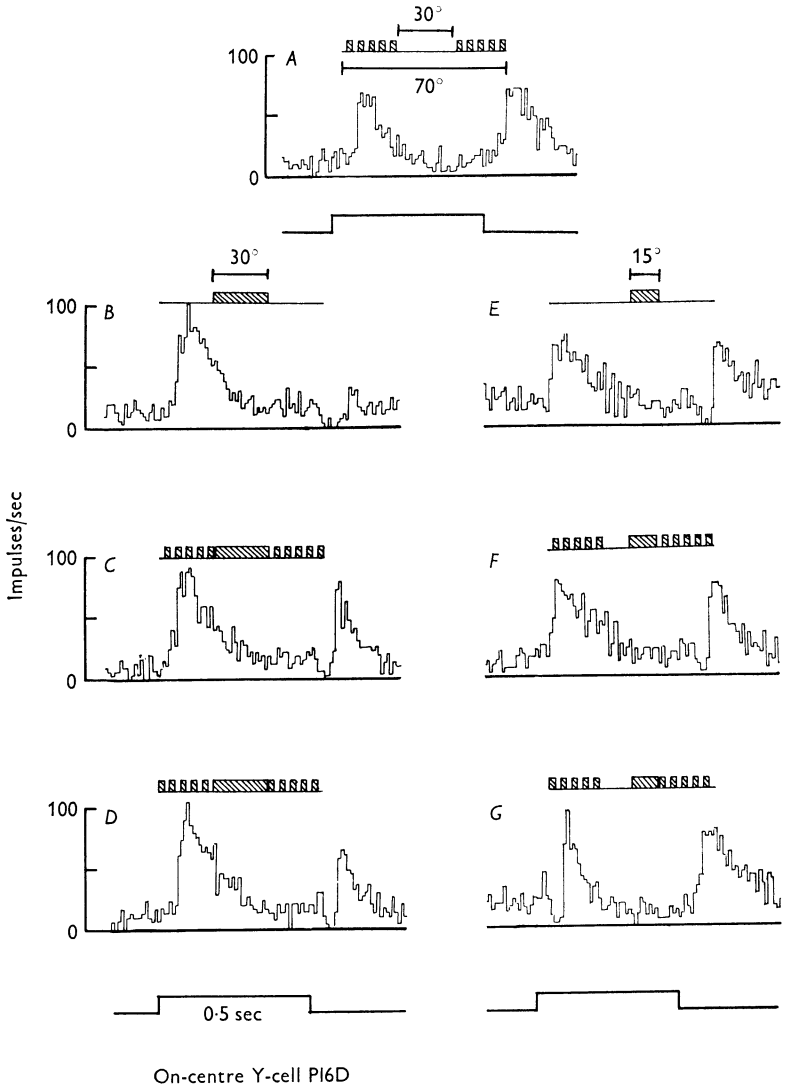
These precautions are still not sufficient to ensure that the light reaching the classical zones of the receptive field is completely unchanged when the grating shifts, so we have done three types of experiment. In the first we argue that, if stray light is the cause, then it should be possible to abolish the response by deliberately adding or removing light from the receptive field synchronously with the move, thus trying to cancel stray light by substitution. In the second type of experiment we deliberately desensitized either the classical receptive field, or the far peripheral retina, by flooding them with continuously applied adapting light, and in the third type we temporarily desensitized these regions by strong bleaching lights which were extinguished during the tests.

Substitution experiments

The movement of a grating might elicit a discharge by altering the amount of light diffusely scattered on to the classical receptive field. If so it ought to be possible to match exactly this change in scattered light by the explicit application or removal of light on the receptive field as the grating is moved. Thus if movement in one direction decreases the amount of light on the receptive field, the simultaneous application of a large spot of appropriate luminance, to ensure a constant flux on the receptive field, will abolish the shift response. Moreover, if that spot is applied together with a movement of the grating in the opposite direction, the shift response ought to be enhanced. This is the logic of the following experiments.

The shift effect is always biphasic, as illustrated in Fig. 1. With Y-type units a small spot placed between the centre and the surround causes a response at both on and off, and so, in some cases, does a diffuse stimulus covering both. Since the stray light postulated to account for the shift is less likely to be focal than diffuse we first used the latter type of stimulus.

In Fig. 2, *A* shows the responses to a shifting grating. *B* is the response



On-centre Y-cell PI6D

Fig. 2. Attempting to compensate for hypothetical changes in stray light by an added stimulus. In all records the spatial configuration is indicated diagrammatically above the trace, and the timing is shown at the bottom of the column or under the trace. *A* shows the response to the shifting grating alone (see Fig. 1 lower right for arrangement of grating). For *B–D* a dim 30° field was turned on and off, and produced excitation at on, weak inhibition of the maintained discharge at off. In *B* there was no shifting grating, in *C* there was, and *D* was the same but with the phase of the shift reversed. In neither case does the dim stimulus reduce the shift response by substituting for the supposed change in stray light. In *E–G* a dim 15° spot was positioned eccentrically to produce a response (*E*) rather like the shift response (*A*), but again it did not reduce the shift response when presented in either phase relation. The bright bars of the grating had luminance 0·4 cd/m², the dark bars 0·2 cd/m², and the 30 and 15° stimuli were also 0·2 cd/m². Histogram details as in Fig. 1.

to a 30° field switched on and off. In this unit the off response was not prominent, but we tried combining it with the grating shift first in one phase (*C*), then the other (*D*). There is no support for the expectation that they would tend to cancel in one phase relation or the other.

Because this unit gave an unsymmetrical response to the 30° field we made further observations with a 15° spot eccentrically placed so that nearly equal on and off responses were obtained (*E*) which matched the shift effect (*A*) quite well. *F* and *G* show the results of combining *A* and *E* in the two phases, and again there is no evidence of cancellation in either of them.

X-type units give a less brisk shift effect, but the weaker responses again occur at both phases of the shift. In these units it is hard to get both on and off responses for any position of stimulus spot, which again argues against the shift responses being caused by stray light.

Continuous adopting fields

The sensitivity of the retina is approximately proportional to the background adapting luminance falling on the region being tested. This effect of background light is not precisely confined to the retinal region upon which it falls (Cleland & Enroth-Cugell, 1968), but the desensitization certainly does not spread more than a few degrees. This provides a tool with which to find out the location of the receptors whose activation causes responses of the type shown in Fig. 1. If these were within the classical receptive field, as the stray light hypothesis states, then adapting light falling on the receptive field should abolish it. If the receptors mediating the response are located in the retina underlying the image of the shifting grating, then adapting light there will reduce the effect.

Fig. 3 shows such an experiment on an on-centre Y-cell. The top pair, *A* and *D*, show responses to a 15° disk centred on the field, and to a remote shifting grating. A 30° bright adapting field was then shone on the centre; *B* shows that this greatly reduced the on response from the 15° disk, and also reduced the weaker off-response. The same adapting field caused a slight increase in the response to the shifting grating (*E*). When adapting light of the same luminance was shone on the remote retina where the shifting grating image fell, as in *F*, the shift effect was very greatly reduced, whereas the on and off responses to the 15° disk (*C*) were only slightly affected.

These adapting experiments have been carried further by measuring thresholds rather than observing the magnitudes of the responses. Fig. 4 shows such results for on-centre (top) and off-centre (bottom) Y-type neurones. A 30° diameter field of variable luminance (abscissa scale) was centred on the receptive field while thresholds for 2° central spots

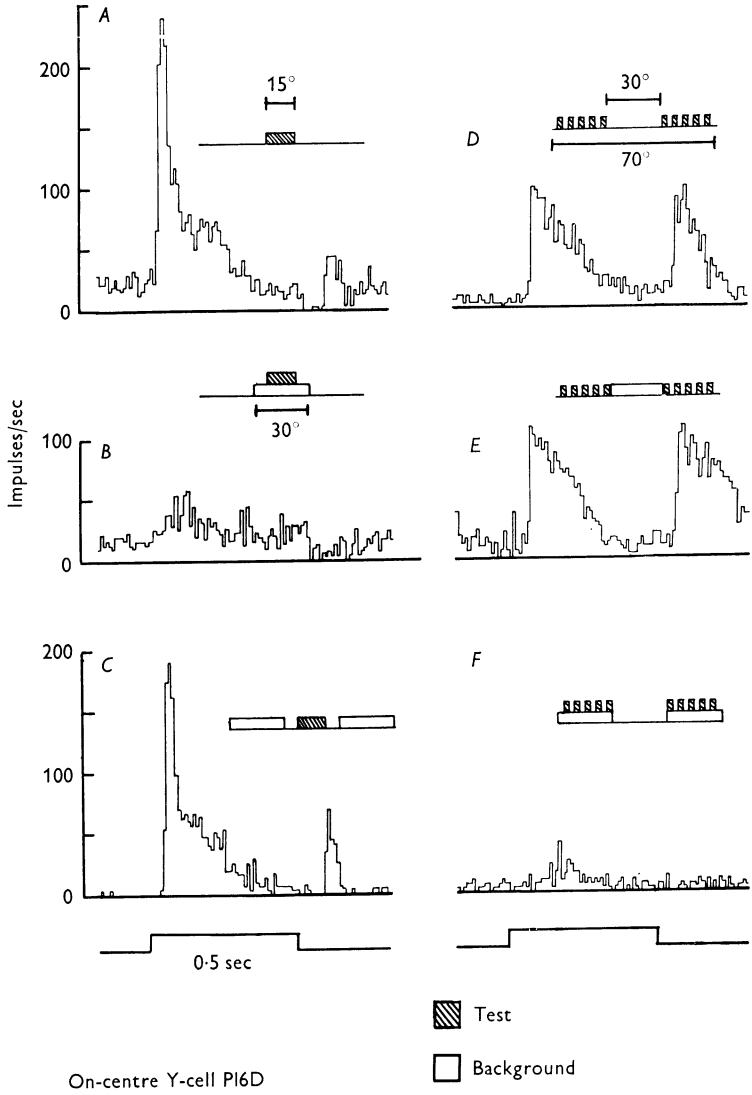


Fig. 3. Reduction of shift response by light adapting the far periphery. Records *A* and *D* show the responses to a 15° disk (luminance 0·2 cd/m²) flashing on to the centre of the receptive field and to a grating (bright bars 0·6 cd/m², dark bars 0·2 cd/m²) moving in the far periphery. In *B* and *E* a bright 30° disk light-adapted the receptive field; this raised the luminance from 0·2 to 3 cd/m² and greatly reduced the response to the 15° disk, but failed to reduce the response to the grating, as it would if this response had been caused by stray light. In *C* and *F* the far periphery was flooded with adapting light at 3 cd/m²; this barely affected the response to the 15° disk (*C*), but greatly reduced the shift response (*F*), which must, then, depend upon excitation of receptors lying 15° or more away from the centre of the receptive field.

(open circles) and the usual annular shifting grating (filled circles) were measured. The thresholds for central spots rise in the usual manner, whereas thresholds for the shift effect are hardly affected by the light falling on the centre.

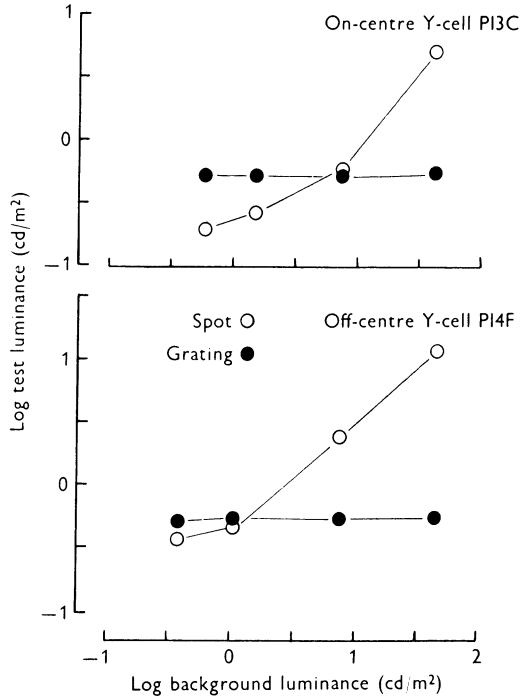


Fig. 4. Effect of 30° diameter adapting field on thresholds for shifting grating (filled circles) and centred stimulus spot (circles). On-centre Y-cell (top); off-centre Y-cell (bottom). The adapting field has the expected desensitization effect on the central stimulus spot, but no influence on the threshold for the shifting grating.

Desensitization by bleaching

One can render receptors insensitive for a period by bleaching a proportion of their photopigment with a very bright light instead of by flooding them with a much weaker continuous light. The advantage of this method is that the sensitivity loss is a rapidly accelerating function of the bleaching exposure, so one can produce almost complete desensitization of one region with very little if any desensitization of other regions resulting from the bleaching caused by scattered light.

Fig. 5 shows an experiment in which first the centre and surround of the receptive field, then the far peripheral retina, were desensitized in this way. Desensitization by bleaching the receptive field elevated threshold

for the classical response (filled circle) while leaving the shift effect almost unaffected (filled square). For peripheral bleaches the differential effect was not so great, but threshold for the shift effect (open square) was elevated more than threshold for a central spot (open circle). This confirms our rejection of scattered light as the factor causing the shift effect.

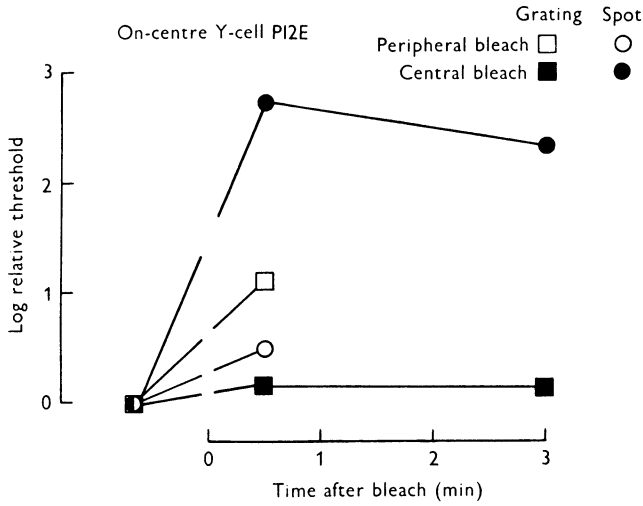


Fig. 5. After-effects of strong central and peripheral adaptations. Filled symbols show the after-effect of a 60 sec bleach produced by 30° central disk at 6200 cd/m² seen through a pupil diameter 3 mm. As expected, the threshold for central stimulation is greatly elevated (filled circles), but threshold for the shift response is only slightly influenced (filled squares). Open symbols show the after-effect of 60 sec bleach of the far periphery at 6200 cd/m² seen through 3 mm pupil diameter; the central 30° was covered with black velvet of low reflectance. Threshold for the shift response was elevated substantially more than threshold for the central spots.

Stimulus/response functions

While attempting these substitution and desensitization experiments there emerged another clear difference between the responses elicited by stimulation of receptive field centre and surround and those elicited from remote regions. This is shown in Figs. 6 and 7. As Fischer *et al.* (1975) found, when the magnitude of the shift response is plotted as a function of the luminance of the inducing grating, the function rises rapidly to a saturating value and shows no change thereafter. On the other hand the response from stimulation of the classical central zone of the receptive field is a much more continuous function of luminance. Fig. 6 shows such responses at three levels of illumination from an on-centre Y-cell; and similar responses over a wider range are plotted out in Fig. 7.

These results show that there is a maximum, fairly low, discharge rate obtainable from the shift effect, but it also has a threshold. For responses from the centre one can define a conventional threshold, where the number of extra impulses becomes reliably discriminable from the fluctuations of

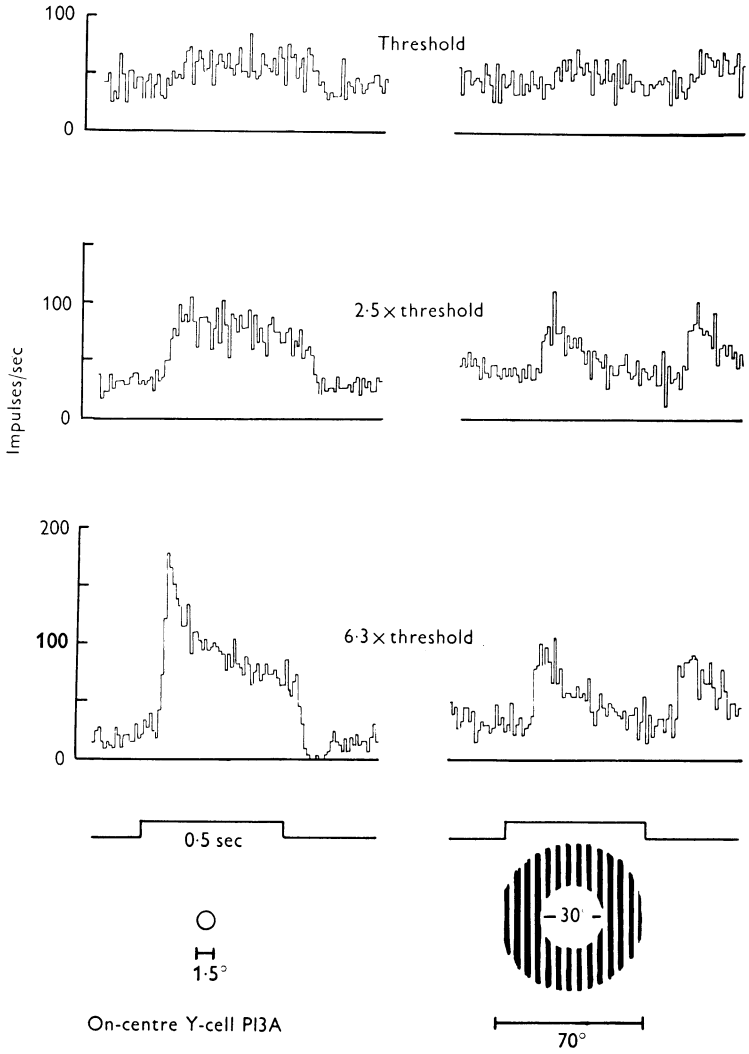


Fig. 6. Gradation of normal and shift responses. As a stimulus is increased from barely detectable (top), through 2·5 × threshold (middle) to 6·3 × threshold (lower) the central stimulus (left) continues to grow in amplitude while the shift responses (right) tend to saturate. Spot luminance at threshold was about 0·2 cd/m² on 0·9 cd/m² background. The shift stimulus was a grating of 90 % contrast added to a constant background of 0·6 cd/m²; at threshold the bright bars of the grating added 0·1 cd/m².

the maintained discharge (Barlow & Levick, 1969), but extra impulses have always been found to be proportional, or less than proportional, to the added stimulus. For the shift effect there is a genuine threshold, and

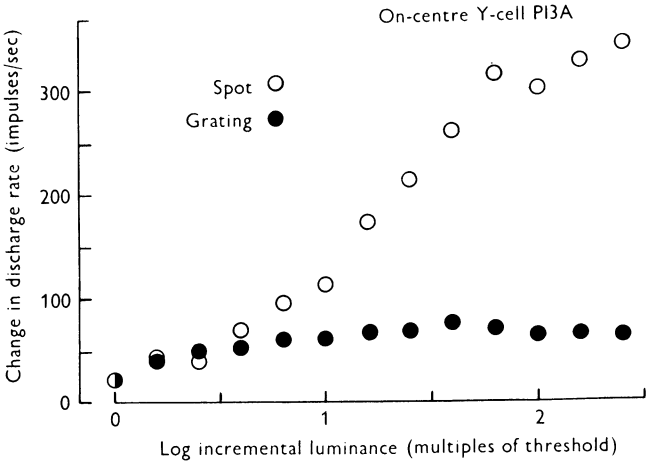


Fig. 7. Changes in peak impulse rate as a function of incremental luminance for responses to central spot (open circles) and shifting grating (filled circles). The grating response does not continue to increase at higher luminances. Luminances of spot and grating and their respective backgrounds are given in Fig. 6 legend.

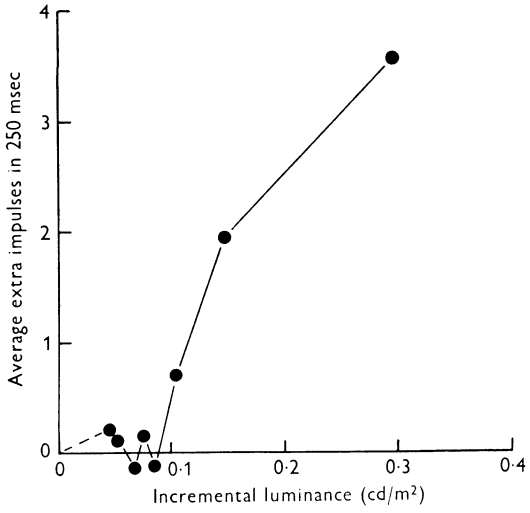


Fig. 8. Extra impulses evoked by shifting a grating of 90 % contrast and variable luminance added to a constant background of 0·2 cd/m². There is a distinct threshold for shift responses when the bright bars add 0·1 cd/m². Responses from the normal receptive field would be linear through the origin on this plot, or show saturating type departures from linearity.

Fig. 8 shows the number of extra impulses elicited by shifting a grating plotted against the luminance of that grating (see legend). There is very clearly a threshold-type non-linearity.

DISCUSSION

Our conclusion from these experiments is that, confirming previous workers, signals from receptors in one retinal region can excite far distant retinal ganglion cells, and when many points are synchronously stimulated these effects can cause the ganglion cells to discharge almost as vigorously and briskly as excitation from the classical receptive field. Intra- or extra-ocularly scattered light does not cause these effects. As for the question of what to call this phenomenon we favour the term *shift effect*, proposed by Fischer & Krüger, because it draws attention to the importance of sudden shifts of the whole visual image in eliciting it under normal conditions. Such shifts would occur with each saccadic movement of the eyes, and we think the mechanism for detecting this global stimulus, and the strong and widespread response it evokes, must be part of a mechanism for dealing with these sudden jumps of the whole visual image.

The shift effect is of course very closely related to the 'periphery effect' discovered by McIlwain (1964, 1966), and probably also the 'rectified responses' recently studied by Hochstein & Shapley (1976). What we had not previously appreciated was the magnitude of the effect and its probable relation to the shifts of the image caused by saccadic eye movements.

Agreements and disagreements

Though we mainly confirm previous reports there are some minor disagreements. Fischer *et al.* (1975) emphasize that, although it is stronger in on-centre units, it is present in all of them, both sustained and transient. Cleland *et al.* (1971) on the other hand say that it is weak or absent in the brisk-maintained (X-type) units, and Ikeda & Wright (1972) agree with this. In X-type units we consistently found a slow waxing and waning of discharge frequency, but only very rarely did we obtain the brisk and vigorous responses we always found in Y-type units. Thus we think the difference lies in the briskness, magnitude, latency and duration of the effect, not in its presence or absence.

Linear spatial summation is a defining characteristic of X-cells, and it is strange they should show any shift responses, which must be due to some non-linear spatial summation. We think that two factors account for this discrepancy. First, tests for linear spatial summation are commonly made using gratings restricted to 15° while the non-linearities revealed by the shift response must, in our experiments, arise from regions beyond

this. We have found a few X-type units that showed the usual linear spatial summation for gratings 15° in diameter, centred on the receptive field, but which displayed definite non-linearity when fields 30° in diameter were used in the normal X–Y test. Secondly, the sluggish shift effect in X-cells would, in many tests, manifest itself only as a slight increase in the mean rate of discharge, and could easily be overlooked.

In the literature there are some contradictions on the effects of steady lights on shift responses (Ikeda & Wright, 1972; Levick *et al.* 1965; Fischer & Krüger, 1974). In our experience steady lights have little influence on the threshold for the shift effect, but they do influence the magnitude of the responses to suprathreshold stimuli, and this may account for previous disagreements.

Mechanism

Dowling & Boycott (1966) suggested that the periphery effect was mediated by the amacrine cells, since there are amacrine–amacrine and amacrine–ganglion cell synapses capable of transmitting effects laterally for the very considerable distances involved. It subsequently transpired (Werblin & Dowling, 1969) that the amacrine cells are excited by temporal transients, sometimes at both on and off, and as Ikeda & Wright (1972) point out this is also characteristic of periphery effects. Furthermore the amacrine cell's stimulus/response function is characteristically short-ranged, as is the shift effect's (Werblin & Copenhagen, 1974; Fischer *et al.* 1975).

One can readily believe that the shift effect is propagated from remote regions by excitatory amacrine–amacrine synapses, and Werblin (1972) has shown that amacrine cells are depolarized by remote shifting stimuli. However, it is not clear whether ganglion cells are excited by amacrine depolarization, as would be required by the hypothesis that they mediate the shift effect, or whether they are inhibited as some of Werblin's results suggest.

Functional role of shift response

Much more information about their central effects is needed before one can be certain that shift responses are part of a mechanism compensating for the sudden movements of the visual image caused by saccadic eye movements. Two suggestions have been made.

Perceptual filling-in. The level of steady illumination in a receptive field is not well signalled by retinal ganglion cells yet we consistently attach white, grey and black sensations to uniform surfaces of high, medium and low reflectance. Neural activity at the edges of uniform fields presumably give rise to this perceptual 'filling-in' and Fischer *et al.* (1975) proposed that the shift effect provides a mechanism for it. This is an

attractive interpretation, based mainly on the influence of bright and dark spots falling in the receptive field centre on the magnitude of the shift response. There is, however, a problem with this suggestion, for when a shift response is generated by a saccadic eye movement the images of small bright or dark spots will move away from the centres of the receptive fields they previously filled. Only if the spots were large would they remain on a receptive field after an eye movement, but large spots do not modify shift responses nearly as effectively as do small ones. It is for large areas that 'filling-in' is perceptually important, but this is where the proposed mechanism fails. Furthermore Moors, Coenen, Gerrits & Vendrik (1974) tested stimuli for their effectiveness in causing 'filling in' when viewing stabilized images. Stimuli which caused strong periphery effects in cats did not produce good filling in and vice versa.

Erasure of previous image. When the eye moves there is a transient discharge from all ganglion cells that depends on change of illumination and not on its absolute value in the new fixation position. Thus in each new fixation position the pattern of impulse frequencies must depend upon the luminance pattern existing in the previous fixation position as well as the new one (Barlow, 1961). Perceptually one sees none of the expected confusion, and the shift effect may be involved in preventing the mixing of the two images. In two respects it is a unique response: first, it occurs synchronously in on- and off-centre units, and these normally work in antiphase. Secondly, an eye movement will generate essentially the same shift-response from every part of the retina. Perhaps central structures interpret this otherwise ungrammatical occurrence as a punctuation mark signifying the end of one fixation position and the beginning of the next, and this unique signal might be used to 'wipe the slate clean' for the next image. MacKay (1970) suggested that it was not the initiation of an eye movement, but the movement of the image over the retina, that caused threshold elevation at the time of a saccade; shift responses may represent the neural signal mediating this effect.

Jung (1975) has made a similar suggestion. If shift responses occur in the human, it is certainly remarkable that we have so little positive awareness of the massive discharges, coming from all the Y-type ganglion cells, which must accompany each saccadic eye movement; one may then reasonably entertain the notion that shift responses have a purely negative effect and serve to suppress the unwanted sensations that might arise with each jerk of the visual scene.

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