

THE MECHANISM OF PERIPHERALLY EVOKED RESPONSES IN RETINAL GANGLION CELLS

BY A. M. DERRINGTON*, P. LENNIE* AND M. J. WRIGHT†

*From the Physiological and Psychological Laboratories,
University of Cambridge, Downing Street, Cambridge CB2 3EG*

(Received 12 June 1978)

SUMMARY

1. Responses to stimulation of retinal regions remote from the classical receptive field were recorded from optic tract fibres in lightly anaesthetized cats.
2. X- and Y-cells gave reliably different responses to the sudden reversal of the phase of a high contrast grating that fell on the retina more than 15 deg from the centre of the receptive field.
3. The mechanism that generates these responses ('shift effect' or 'periphery effect') in Y-cells is insensitive to the spatial phase of the stimulating grating. It can resolve gratings of higher spatial frequency than can be resolved by the classical receptive field mechanisms of Y-cells but its temporal resolution is poorer.
4. Signals that contribute to peripherally evoked responses are accumulated over a region that extends to at least 35 deg from the centre of the receptive field. Although this region is not uniformly sensitive, regions in the periphery of the visual field are as effective as regions around the area centralis in eliciting the responses, and do not require coarser gratings.
5. In some Y-cells the response to peripheral stimulation was amplified by increasing (on-centre units) or decreasing (off-centre units) the steady illumination of the centre of the receptive field. This confirms Krüger & Fisher (1973), but the effect is only found in a proportion of cells.
6. The mechanism that generates peripherally evoked responses is tentatively identified with the 'rectifying subunits' postulated by Hochstein & Shapley (1976b) to account for the spatial non-linearity in the receptive fields of Y-cells. Transient (bistratified) amacrine cells are known to have many of the properties attributed to these mechanisms (Chan & Naka, 1976).

INTRODUCTION

McIlwain (1964) demonstrated that the movement of a stimulus in the visual field far from the classically defined receptive field of a retinal ganglion cell led to a modest, relatively steady, discharge of impulses. He named this the 'periphery effect', which Levick, Oyster & Davis (1965) later showed did not result from light

* Present address: Laboratory of Experimental Psychology, University of Sussex, Falmer, Brighton, England.

† Present address: Department of Psychology, Brunel University, Uxbridge, England.

scattered on to the receptive field. Subsequently McIlwain (1966) demonstrated short-latency responses (< 100 msec) to sudden movement of contours well outside the receptive field. Ikeda & Wright (1972) made explicit the distinction between this *modulated* periphery effect, and the *unmodulated* periphery effect of McIlwain's earlier experiment. Later, Krüger & Fischer (1973) obtained from some cells responses as vigorous as those resulting from stimulation of just the centre of the receptive field when they shifted by one half-period a grating that covered nearly the whole visual field except an area 40 deg in diameter centred on the receptive field. They give the name 'shift effect' to these discharges, which Barlow, Derrington, Harris & Lennie (1977) showed could not be artifacts due to stray light, but must result from the activity of neural mechanisms that accumulate signals from a large retinal area.

The shift effect probably has its origin in the same mechanism that generates the 'modulated' periphery effect (Fischer, Krüger & Droll, 1975) but it is not clear whether the 'unmodulated' periphery effect has a similar origin.

In this paper we examine the relationship between the shift effect ('modulated' periphery effect) and the 'unmodulated' periphery effect found by McIlwain (1964) and Ikeda & Wright (1972). We also describe in more detail the spatial organization of the mechanism that generates this discharge, and its relevance to the distinction between X- and Y-cells (Enroth-Cugell & Robson, 1966).

METHODS

The methods used were the same as those described fully in Barlow *et al.* (1977): the activity of ganglion cells was recorded from axons in the optic tract of cats lightly anaesthetized with urethane, and paralysed with gallamine triethiodide (Flaxedil). A PDP 11/10 computer controlled the presentation of stimuli and monitored the discharges of cells.

Detailed records were obtained from twenty-nine cells in twelve cats. All except two were classified as X-(brisk-sustained) or Y-(brisk-transient) cells using the methods described in Barlow *et al.* (1977).

Definitions

Throughout this paper we used the term 'receptive field' to denote the centre and surround regions described by Kuffler (1953). Remote regions (more than 15 deg from the centre of the receptive field) where stimulation gives rise to a response from the cell are also strictly part of this receptive field but, because we believe the mechanisms to be different, we refer to them as the *periphery*.

RESULTS

Peripherally evoked responses in X- and Y-cells. After identification of a cell as X or Y, an attempt was made to elicit responses from the periphery using a square-wave grating of contrast 50% and spatial frequency 0.18 c/deg. This was back-projected on to the tangent screen and an occluder, diameter 30 cm, was placed on the front of the screen and centred on the receptive field, ensuring that no part of the grating fell within 15 deg of the centre (see inset to Fig. 1). The response was elicited by abrupt displacement of the grating by one half-period. After the discharge had subsided the grating was equally abruptly restored to its original position. Equal responses were obtained following displacements in both directions. Since these

responses are usually brief, their magnitude is conveniently measured as the difference between the number of impulses discharged in the 100 msec period spanning the peak of the discharge and the number discharged in a corresponding interval at the end of the period (usually 3 sec) for which the grating was stationary. Fig. 1 shows, separately for X- and Y-cells, the frequency with which responses of a given size occurred in the units of the sample studied.

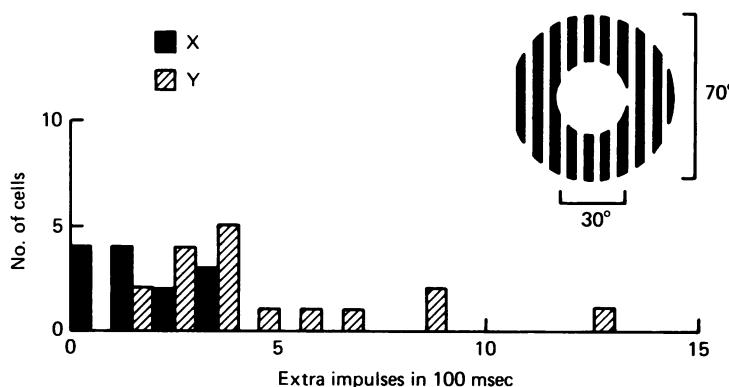


Fig. 1. Magnitude of peripherally evoked responses in X- and Y-cells. A square-wave grating, frequency 0.18 c/deg was back-projected on to a tangent screen through a circular aperture. It covered a retinal region 70° in diameter centred on the receptive field, but was occluded from the receptive field by a concentric disc 30° in diameter and luminance 0.2 cd.m⁻² (inset). Responses were elicited by an abrupt displacement of the grating by one half-period. Ordinate: number of impulses discharged in 100 msec following grating displacement minus number discharged in 100 msec preceding displacement, averaged over thirty trials. Contrast, 50% mean luminance 1 cd.m⁻². Pupil dilated.

The histograms show that although the presence of a peripherally evoked response does not dichotomize X- and Y-cells unequivocally, responses are reliably stronger in the latter (Y-cells; mean = 4.8 extra impulses in 100 msec; X-cells, mean = 1.9 extra impulses; $t = 3.1$, 27 d.f., $P < 0.01$). This confirms Cleland, Dubin & Levick (1971). The distinction between X- and Y-cells may be even more sharply made if the phase of the grating is reversed faster than twice per second, for the mechanism in X-cells is noticeably more sluggish (Barlow *et al.* 1977).

The relatively weak response seen in X-cells (Fig. 1) even when a large area of retina is stimulated by a grating, and its relatively sluggish nature are probably the reasons why Ikeda & Wright (1972) found such responses only in Y-cells.

Relation to periphery effects. Barlow *et al.* (1977) found that in X-cells the response to shifts of a grating was often too sluggish to manifest itself as a discrete discharge following the movement of a grating every half-second, but appeared as a relatively uniform elevation of the maintained discharge. The question then arises whether the 'unmodulated' periphery effects found in Y-cells (McIlwain, 1966; Ikeda & Wright, 1972) represent the activity of the mechanism that generates the 'modulated' periphery effect (shift effect) but stimulated by faster rates of movement. When the response is elicited by a grating that moves every half-second, discrete responses that decay over about 0.3 sec are obtained from a Y-cell (Fig. 2A) but when the rate

of movement is raised to 14 Hz the discrete responses merge into a steady discharge (Fig. 2B), appreciably greater than the maintained discharge in the absence of the oscillation (Fig. 2C).

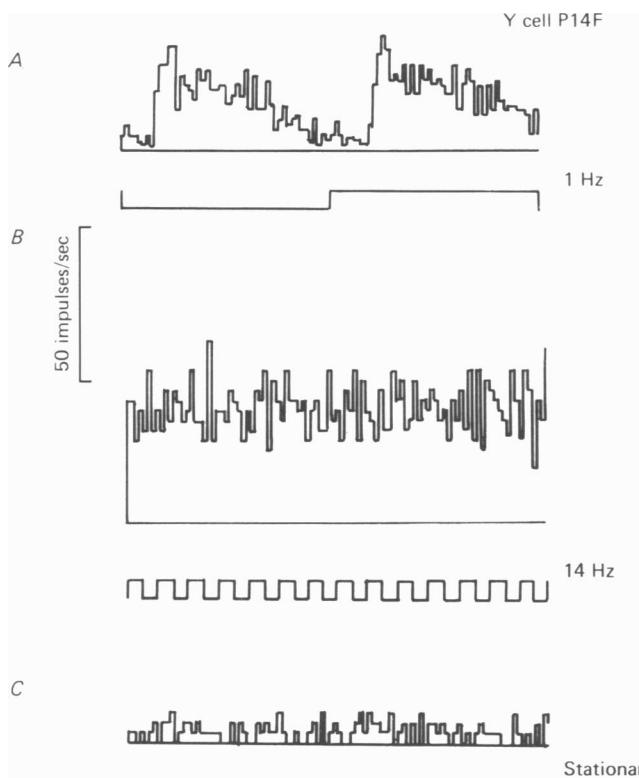


Fig. 2. Effect of alternation rate on peripherally evoked responses. A, response to the shift of a grating by one half-period every 500 msec. B, response to the shift by one half-period every 36 msec. C, response to a stationary grating. The stimulus configuration was as shown in the inset to Fig. 1. Contrast, 50 %, mean luminance 1 cd. m^{-2} . Histograms are accumulated responses to thirty presentations of the stimulus. Bin width 10 msec.

This poor temporal resolution of the mechanisms in the periphery probably contributes to the 'unmodulated' periphery effect, for the experiments that demonstrated it (McIlwain, 1964; Ikeda & Wright, 1972) used hand-held patterns moving in broad sweeps at speeds of 10–20 deg/sec.

The mechanism that generates these responses must possess a rectifying non-linearity since the response to the shift of a grating by one half-period is the same as the response to an equal and opposite shift. Moreover, this mechanism must integrate the effects of illumination over small areas, otherwise it would not generate responses to movement of relatively fine gratings.

Several lines of evidence suggest that these areas of integration are densely distributed. First, responses to shifts are equally strong whatever the spatial phase of the grating in relation to the retina; secondly, when we explored small regions in the periphery with a single, short, bright bar that was stepped between two adjacent positions, we did not find asymmetries in the strength of the responses; thirdly,

sinusoidal grating patterns that drift in the periphery never give rise to a modulated discharge from a unit, whatever the rate of drift. These patterns always bring about a modest increase in the steady discharge.

These findings are all consistent with the notion that the peripheral response generator possesses small densely packed areas of integration – properties that make it easy to understand how this mechanism, when stimulated appropriately, could give rise to both the 'modulated' and 'unmodulated' periphery effects; a step change in grating position stimulates all response generators at the same instant and will thus give rise to a discrete response. But a grating that drifts across the periphery excites different response generators asynchronously and the discrete responses from each generator fuse into a steady discharge.

These properties resemble those of the mechanism that contributes the spatially non-linear component to the discharges of Y-cells when the classical receptive field is stimulated (Hochstein & Shapley, 1976b). The following experiments provide evidence on further similarities.

Spatial properties of the peripheral response generator

Size of integration areas. The presumptive overlap of integration areas makes it hard to establish whether the peripheral mechanisms that generate responses are wholly rectifying, i.e. respond both to an increase and to a decrease in illumination, or are partially rectifying and each respond only to an increase or to a decrease in illumination.

It is, however, possible to say something of the size of the integration areas, and whether or not they have a spatially opponent structure, by measuring the contrast sensitivity to grating patterns of several spatial frequencies.

In the following experiments sinusoidal gratings, displayed on the face of an oscilloscope, stimulated the periphery. The display subtended 15×15 deg and was positioned so that its near edge lay 15 deg from the centre of the receptive field (inset, Fig. 3). Since the peripheral response is insensitive to the spatial phase of the stimulating patterns it could conveniently be evoked by a sudden reversal of phase of the sinusoidal grating (1 Hz). The experimenter adjusted the contrast of the grating until responses to phase reversals were just audible. Each threshold setting was recorded by the computer, which then presented a new spatial frequency randomly chosen from the previously determined range. Four estimates of threshold were obtained at each spatial frequency. Reciprocal thresholds from an experiment on one Y-cell are plotted as the open circles in Fig. 3A.

We also examined the contrast sensitivity of the receptive field proper but, because the response is sensitive to the spatial phase of the grating (Enroth-Cugell & Robson, 1966), and it was difficult to guarantee long-term stability of the eyes, we used a grating that drifted continuously across the receptive field at 2 Hz and the experimenter set the contrast for an audible modulation of discharge. The filled circles in Fig. 3A plot the contrast sensitivity based on these measurements. Fig. 3A shows that peripheral mechanisms are most sensitive to spatial frequencies around 0.2 c/deg, while the receptive field mechanisms preferred gratings of slightly lower frequency. Comparable measurements were made on thirteen more Y-cells and 4 X-cells, and Fig. 3B shows some results from one of the latter.

Differences between the spatial selectivity of the receptive field proper and of the periphery are conveniently characterized by finding the upper and lower spatial frequencies at which contrast sensitivity has declined by a criterion amount. For each cell the high-frequency point was taken as the frequency at which contrast

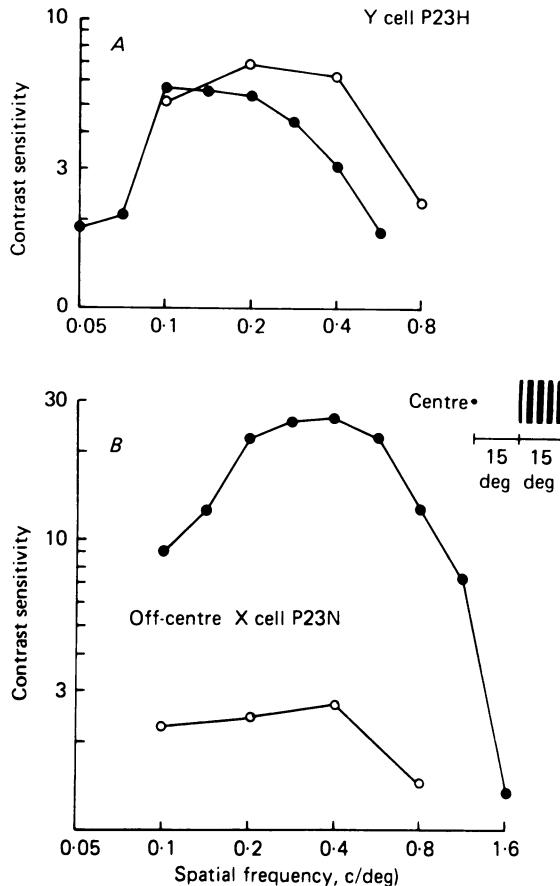


Fig. 3. Contrast sensitivity curves for the peripheral mechanism (open circles) and the receptive field (filled circles) in (A) an on-centre Y-cell, and (B) an off-centre X-cell. Inset shows the stimulus configuration. To elicit the peripheral response a sinusoidal grating of 15 deg in diameter was centred 22.5 deg from the receptive field centre, and its phase was reversed at 2 Hz. To stimulate the receptive field the grating was centred on it, and drifted across it at 2 Hz. Mean luminance 200 cd. m⁻². 3 mm artificial pupil. ○, Periphery; ●, receptive field.

sensitivity had declined by a factor of 2, and was read from continuous curves fitted by calculating three-point weighted averages for data points and computing a spline interpolation between them (Pennington, 1970).

The criterion spatial frequency for the periphery ranged between 0.44 and 0.84 c/deg in different units, about a mean of 0.63 c/deg, while the corresponding values for the receptive field proper ranged between 0.29 and 0.82 c/deg about a mean of 0.44 c/deg. The two sets of values were consistently related: in all the Y-cells on which both sets of measurements were made the critical frequency for the periphery was close to 1.6 times that for the receptive field proper.

We were unable to measure reliably the contrast sensitivity in the periphery to gratings of lower frequency than 0.1 c/deg because phase reversals of the grating produced appreciable changes of flux in the 15 deg field, and these were sometimes sufficient to stimulate the receptive field. Nevertheless, in no retinal region studied

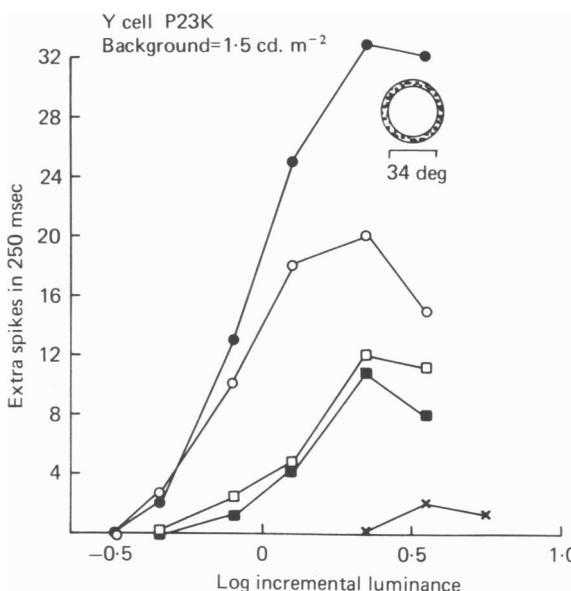


Fig. 4. Stimulus-response relations for peripherally evoked responses at different distances from the receptive field. Responses were elicited by a step rotation, concentric with the receptive field, of annular patterns made up from randomly juxtaposed black and white squares 0.6 deg on the side (inset). All annuli were equal in area, but formed a series with increasing diameters. Ordinate: discharge in the 250 msec following the step rotation of the annulus minus discharge in the 250 msec preceding this step. Abscissa: log incremental luminance of the bright dots (cd. m^{-2}) (pupil dilated). Background, 1.5 cd. m^{-2} . Internal diameters of annuli: (●—●) 34.1 deg; (○—○) 46.9 deg; (□—□) 56.0 deg; (■—■) 63.1 deg; (×—×) 68.9 deg.

did mechanisms in the periphery show any significant loss of sensitivity at spatial frequencies down to 0.1 c/deg. This suggests that, at least under the temporal conditions used in our experiments, there is negligible spatial antagonism within the 'receptive fields' of response generators.

Region from which signals are accumulated. We investigated this using annular stimuli constructed from random dot patterns. These annuli, all of equal area on the tangent screen, formed a series with increasing internal and external diameters and stimulated areas of retina at different distances from the centre of the receptive field. Each annulus was filled with a matrix of black and white squares (side 0.6 deg) randomly juxtaposed.

Abrupt rotation of an annulus through 5 deg elicited a response indistinguishable from that generated by displacement of a grating. Since the response can be generated by rotation about the centre of the receptive field it cannot arise from a mechanism that accumulates signals uniformly from a region concentric with the receptive field.

Fig. 4 shows a series of stimulus-response relations obtained from one unit using

random-dot annuli of different diameters but equal area. The maximum response obtained declined progressively with increasing annulus diameter (i.e. increasing distance from the centre of the receptive field) although the threshold changed little until the inner diameter of the annulus reached 68.9 deg where sensitivity was much

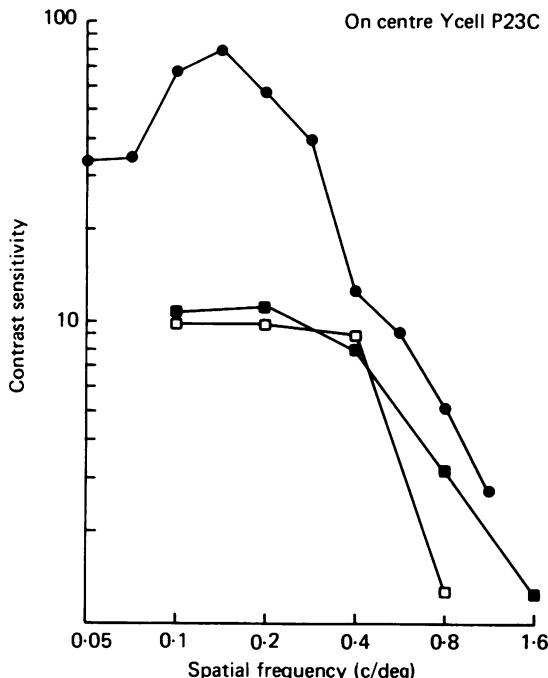


Fig. 5. Contrast sensitivity curves for the receptive field (filled circles) and the peripheral mechanism elicited from the area centralis (open squares) and 40 deg from the area centralis (filled squares), in an on-centre Y-cell. To stimulate the receptive field, a 15 deg diameter grating was centred on the receptive field and drifted at 2 Hz. To elicit the peripherally evoked response, the same grating was centred 20 deg from the receptive field centre on the area centralis, or on the opposite side of the receptive field, 40 deg in the peripheral retina, and its phase was reversed at 2 Hz. Mean luminance 200 cd. m⁻². Dilated pupil. ●, Receptive field; □, area centralis; ■, 40 deg periphery.

reduced, possibly as a result of poor imagery. The slight decline in response to the strongest stimuli occurred frequently (cf. Barlow *et al.* 1977, fig. 7).

The largest annuli used in this experiment stimulated regions some 35 deg (7 mm; Bishop, Kozak & Vakkur, 1962) from the centre of the receptive field, and the smallest fell 17 deg from the receptive field. Over this distance we were unable to resolve differences in response latencies (less than 10 msec), which suggests that the conduction velocity of the mechanisms that propagate the response must exceed 0.33 m/sec. This is close to the value (0.35 m/sec) deduced by Fischer *et al.* (1975) from different experiments.

Consequences of retinal inhomogeneity. As the sensitive periphery may cover a region of 100 deg or more in diameter, parts of it fall on the area centralis while other parts of it may be in far peripheral retina, where the retinal mosaic is much coarser. For eight units we measured contrast sensitivities at different points on the

retina that were equal distances from the centre of the receptive field, but in no case did we observe any reduction in spatial resolution of the type one might expect, although in one unit sensitivity was lower in the peripheral retina. Fig. 5 shows a particularly fortunate example in which the receptive field lay 20 deg from the area

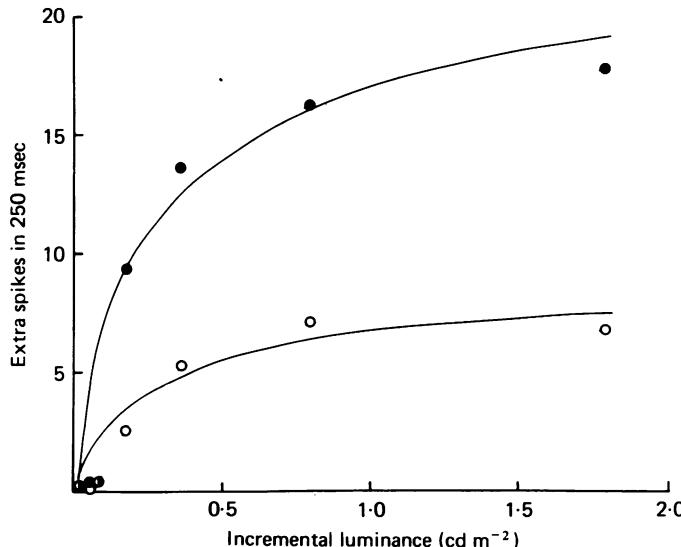


Fig. 6. Stimulus-response relation for the peripherally evoked response in the presence and absence of a steady spot on the centre of the receptive field. The stimulus configuration is shown in the inset to Fig. 1. Responses were elicited by shifting the spatial phase of the grating by one half-cycle every 500 msec. Ordinate: impulses discharged in the 250 msec following the shift of the grating minus impulses discharged in the 250 msec preceding the shift. Abscissa: incremental luminance of the bright bars of the grating (grating background, 1.0 cd.m^{-2} ; luminance of central 30 deg region, 0.11 cd.m^{-2} , Filled circles: responses obtained with a steady spot, diam. 1.5 deg, luminance 2.4 cd.m^{-2} , centred on the receptive field. Open circles: responses in the absence of the small spot. The smooth curves are loci of eqn. (1) with only the scale factor K different in the two cases. On-centre Y-cell p17H. ●, Spot on centre; ○, no spot.

centralis. It was possible then to measure contrast sensitivity both at the area centralis and 40 deg in the peripheral retina. Sensitivity was equal in the two places.

Interactions with classical receptive field. Krüger & Fischer (1973) reported that 'adequate illumination' of the centre of the receptive field (steady bright spots for on-centre units, dark spots for off-centre ones) increased the amplitude of the shift effect. We examined this interaction in twenty-two cells (thirteen X and nine Y) and found positive effects in eleven of them (four X and seven Y).

Fig. 6 shows stimulus-response relations for an on-centre Y-cell in which steady illumination of the receptive field amplified the response to stimulation in the periphery. A grating that covered the whole visual field except for an area 30 deg in diameter centred on the receptive field was shifted one half-period every half-second. Filled circles show the relation obtained when the centre of the receptive field was stimulated by a steady spot 1.5 deg in diameter; open circles show the relation without the spot.

Both relations are characteristically short-ranged, with an apparent threshold at

around 0.05 cd.m^{-2} and saturation at around 0.8 cd.m^{-2} (Barlow *et al.* 1977), but responses are appreciably stronger when the centre of the receptive field is illuminated.

The nature of the change in response brought about by illumination of the centre can be seen by considering eqn. (1), which describes the relation shown in Fig. 6.

$$R = K \left(1 - \frac{1}{1 + CS^{0.6}} \right). \quad (1)$$

R is the peak discharge rate, S the incremental illumination and C a constant. The scale factor K is different in the two cases, which suggests that illumination of the centre of the receptive field may regulate the output of the peripheral mechanism that generates the responses. Had this illumination acted on the input to the response generator, i.e. as if the luminance of the grating had been changed it ought to have been possible to superimpose the two sets of points by scaling one on the abscissa. Clearly this cannot be done.

Eqn. (1) does not produce a threshold discontinuity, although the stimulus-response relation is very steeply accelerated at low luminances. The observations in Fig. 6 make it easy to understand why Barlow *et al.* (1977) found little influence of spot luminance on thresholds determined by listening: the grating luminance required for the criterion response of one or two extra impulses is little altered by illuminating the centre of the receptive field. Only when high-contrast gratings are used does central illumination have a strong effect on responsiveness.

DISCUSSION

Difference between X- and Y-cells. Our results show clearly that the periphery effect/shift effect is present in some X- as well as in Y-cells, although in the former it is weak and sluggish. In X-cells it has often gone unnoticed, probably because the mechanism responsible is absent or inconsequential close to the receptive field; were it present to any appreciable degree, the discrimination between X- and Y-cells could not be reliably based upon the linearity of spatial summation (Enroth-Cugell & Robson, 1966; Hochstein & Shapley, 1976a).

Our experiments provide a number of hints about the nature of the mechanisms that generate responses to stimulation in the periphery: they integrate the effects of light over areas of diameter up to 1 deg and are densely packed and possibly overlapping; they also have thresholds and generate signals that are rapidly saturating functions of luminance. These signals are then combined non-linearly.

Several of these properties parallel those of the 'rectifying subunits' that Hochstein & Shapley (1976b) have postulated to account for the non-linear spatial summation found in the receptive field of Y-cells, and it is worth while to consider whether the mechanisms could be the same. Important evidence on this comes by comparing contrast sensitivity curves obtained by stimulating the receptive field proper with those obtained by stimulating the periphery some 15 deg away.

Hochstein & Shapley (1976b) found from contrast sensitivity curves that the mechanism that contributed the second harmonic component to the discharge of Y-cells could resolve gratings of spatial frequency about three times higher than could be resolved by the receptive field mechanisms that generated the fundamental response. Our results show that the spatial resolution of the peripheral response

generator is about 1.6 times that of receptive field mechanisms. We compared frequencies at which sensitivity had declined by a factor of 2 from its peak, and the different indices of resolution used may largely account for the discrepant results, since R. M. Shapley & J. D. Victor (personal communication) find that the loss of second-harmonic sensitivity at high spatial frequencies is more gradual than the loss of sensitivity of linear receptive field mechanisms.

The short-ranged stimulus-response relationship found in the periphery also characterizes the second harmonic (rectifying) component in the discharges recorded from Y-cells stimulated in the receptive field proper (Hochstein & Shapley, 1976*b*, Fig. 7). Both mechanisms are insensitive to the spatial phase of grating patterns, and both generate short-lasting discharges to a change of stimulus. Finally, Hochstein & Shapley's measurements suggest that the source of the rectified component in discharges of Y-cells extends well beyond the boundaries of the conventional receptive field; this fits our observations well.

Cleland *et al.* (1971) first drew attention to the presence of a strong periphery effect in Y-cells, and used it as one means of distinguishing them from X-cells. The results of Fig. 1 suggest that a reliable distinction may be made on the basis of responses to shifts of gratings in the periphery. This will be especially the case if shifts occur more rapidly than two per second, an alteration rate not followed well by the peripheral mechanism of X-cells.

Mechanism. Amacrine cells have been implicated both in the generation of the periphery effect/shift effect (Dowling & Boycott, 1966; Ikeda & Wright, 1972; Barlow *et al.* 1977) and in the rectifying non-linearity described by Hochstein & Shapley (1976*b*). On structural grounds this is plausible because only amacrine and horizontal cells have the presumed lateral interconnexions necessary for propagation of signals over large areas of retina (Boycott & Dowling, 1969). We can exclude horizontal cells as candidates because rectification in their behaviour would be reflected in the behaviour of bipolar cells and thus in ganglion cells. But we know that the centre and surround mechanisms of most X-cells, and probably also the conventional receptive field mechanisms in Y-cells (Hochstein & Shapley, 1976*b*) show no non-linearity like that found in the periphery, and it is hard to see how that could happen if bipolar cells were other than linear. Furthermore, our results suggest that the response generator in the periphery has no spatially antagonistic structure. Bipolar cells are known to have concentrically organized receptive fields, but most amacrine cells apparently do not (Burkhardt, 1975; Chan & Naka, 1976). Finally, one class, the bistratified amacrine cell (Cajal, 1893) or transient neurone (Chan & Naka, 1976) always gives a frequency-doubled response to sinusoidal stimulation. It is this cell, which seems to be present in all vertebrate retinas (Naka, 1976) that we suspect is important in the generation of the responses from regions beyond the classical receptive field of Y-cells: the transient neurone generates responses that are independent of stimulus intensity and size over a wide range.

It is tempting to suppose that the threshold in the periphery reflects the threshold of this cell for initiation of its transient potential and that the very limited response range in the periphery (fig. 7, Barlow *et al.* 1977) reflects the fact that the transient potential is regenerative (Werblin, 1977) and may function like an action potential with respect to its all-or-none properties.

The much weaker and more sluggish response found in X-cells suggests that in

these units a different mechanism is responsible. Possibly the sustained neurones of Chan & Naka (1976) ('true' amacrine cells) are involved in this, but these units do not generate the same responses to light onset and offset, so some additional rectification would be required between them and an X-cell.

We are grateful to Professor H. B. Barlow for valuable advice. This work was supported by grants from the M.R.C. to H. B. Barlow and C. Blakemore, and by a grant from the Royal Society to H. B. Barlow. A. M. Derrington held an M.R.C. studentship.

REFERENCES

BARLOW, H. B., DERRINGTON, A. M., HARRIS, L. R. & LENNIE, P. (1977). The effects of remote retinal stimulation on the responses of cat retinal ganglion cells. *J. Physiol.* **269**, 177-194.

BISHOP, P. O., KOZAK, W. & VAKKUR, G. J. (1962). Some quantitative aspects of the cat's eye: axis and plane of reference, visual field co-ordinates and optics. *J. Physiol.* **163**, 466-502.

BOYCOTT, B. B. & DOWLING, J. E. (1969). Organization of the primate retina. Light microscopy. *Phil. Trans. R. Soc. B* **255**, 109-184.

BURKHARDT, D. A. (1975). A nascent electrophysiology of amacrine cells. *Investive Ophth.* **14**, 171-173.

CAJAL, S. R. Y. (1893). *The Vertebrate Retina* (translated by D. MAGUIRE & R. W. RODIECK). In RODIECK, R. W., *The Vertebrate Retina*. San Francisco: Freeman (1973).

CHAN, R. Y. & NAKA, K.-I. (1976). The amacrine cell. *Vision Res.* **16**, 1119-1129.

CLELAND, B. G., DUBIN, M. W. & LEVICK, W. R. (1971). Sustained and transient neurones in the cat's retina and lateral geniculate nucleus. *J. Physiol.* **217**, 473-496.

DOWLING, J. E. & POYCOTT, B. B. (1966). Organization of the primate retina: electron microscopy. *Proc. R. Soc. B* **166**, 80-111.

ENROTH-CUGELL, C. & ROBSON, J. G. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *J. Physiol.* **187**, 517-552.

FISCHER, B., KRÜGER, J. & DROLL, W. (1975). Quantitative aspects of the shift effect in cat retinal ganglion cells. *Brain Res.* **83**, 391-403.

HOCHSTEIN, S. & SHAPLEY, R. M. (1976a). Quantitative analysis of retinal ganglion cell classifications. *J. Physiol.* **262**, 237-264.

HOCHSTEIN, S. & SHAPLEY, R. M. (1976b). Linear and nonlinear spatial subunits in Y cat retinal ganglion cells. *J. Physiol.* **262**, 265-284.

IKEDA, H. & WRIGHT, M. J. (1972). Functional organization of the periphery effect in retinal ganglion cells. *Vision Res.* **12**, 1857-1879.

KRÜGER, J. & FISCHER, B. (1973). Strong periphery effect in cat retinal ganglion cells. Excitatory responses in on- and off-centre neurones to single grid displacements. *Expl Brain Res.* **18**, 316-318.

KUFFLER, S. W. (1953). Discharge patterns and functional organization of mammalian retina. *J. Neurophysiol.* **16**, 37-68.

LEVICK, W. R., OYSTER, C. W. & DAVIS, D. L. (1965). Evidence that McIlwain's periphery effect is not a stray light artefact. *J. Neurophysiol.* **28**, 555-559.

MCILWAIN, J. T. (1964). Receptive fields of optic tract axons and lateral geniculate cells: peripheral extent and barbiturate sensitivity. *J. Neurophysiol.* **27**, 1154-1173.

MCILWAIN, J. T. (1966). Some evidence concerning the physiological basis of the periphery effect in the cat's retina. *Expl Brain Res.* **1**, 265-271.

NAKA, K.-I. (1976). Neuronal circuitry in the catfish retina. *Investive Ophth.* **15**, 926-935.

PENNINGTON, R. H. (1970). *Introduction to Computer Methods and Numerical Analysis*, 2nd edn. London: Collier MacMillan.

WERBLIN, F. S. (1977). Regenerative amacrine cell depolarization and formation of on-off ganglion cell response. *J. Physiol.* **264**, 767-785.