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NEW PROPERTIES OF RABBIT RETINAL GANGLION CELLS

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SUMMARY

1. Receptive fields of centre surround cells in the rabbit retina were investigated. There is a clear distinction between cells with sluggish responses, low spontaneous activity and slow conduction velocity (centre surround sluggish cells) and cells with brisk responses, higher spontaneous activity and faster conduction velocity (X and Y cells). The sluggish cells can be divided into sustained and transient types. X and Y cells can be distinguished from each other by their responses to a moving linear grating, a large rapidly moving object and whether or not there is a response to the alternation of certain stimuli. Sometimes the response to a rotating radial grating, the rate of spontaneous activity, and whether or not the response to spots and annuli was sustained or transient could also be used to distinguish these two types. The antidromic latency from electrical stimulation of the optic chiasm and the periphery effect did not distinguish X from Y.

2. Eleven colour coded units were investigated. They all gave on responses to blue light in the centre of their receptive field and off responses to green light in the periphery of their receptive field. The blue pigment had a spectral sensitivity peaking at about 465 nm. The other pigment peaked near 500 nm, like the rods, but gave a response at high mesopic and probably photopic levels. In some cases there was evidence for an excitatory input from the green receptors to the centre of the receptive field. All the colour coded cells had rapidly conducting axons and were on centre X cells by all criteria.

3. Eighty-five cells of various types other than colour coded were tested for their thresholds at 420 nm and 590 nm. In all cases the results were explained by a pigment peaking close to 500 nm, even at high mesopic and low photopic levels, which suggests the existence of cones with a cyan pigment in them.

4. Conduction latency from stimulation at the optic chiasm was measured for cells with centre surround receptive fields and cells with more complex receptive fields. Both 'on–off' and 'on' directionally sensitive cells have short conduction latencies, overlapping X and Y cells. Orientation selective cells and local edge detectors have long conduction latencies, overlapping centre surround sluggish cells. The sample of uniformity detectors was too small to characterize.

5. Two generalizations made from studies with cat were not found to hold in the rabbit. One cannot make the generalization that cells with more complex types of

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receptive field have a slow conduction velocity because of the results with directionally selective cells. One cannot make the generalization that cells which respond only to slow movements and have low spontaneous activity have a slow conduction velocity because of the results with the 'on' directionally selective cells and a class of 'on' centre sustained cells called hybrid units, because they had sluggish receptive field properties and fast conduction velocities. The correlation between receptive field type and latency from antidromic stimulation at the optic chiasm therefore varies with the species of animals tested.

INTRODUCTION

In many respects, the receptive fields of ganglion cells in the rabbit retina have been very well studied. Directionally sensitive ganglion cells have been characterized best in the rabbit retina (Barlow, Hill & Levick, 1964), with a number of tests to prove that their directionality is not an artifact (Barlow & Levick, 1965). Other types of cell with complex receptive fields, such as local edge detectors, uniformity detectors, and orientation selective cells, have also been thoroughly characterized in the rabbit (Levick, 1967).

However, the analysis of cells with centre surround receptive fields has been carried much further in the cat than in the rabbit. Enroth-Cugell & Robson (1966) suggested the division of centre surround cells into X and Y types, based on whether spatial summation within the receptive field is linear or not. This distinction has since been shown to correlate with a number of other receptive field properties, and with the conduction velocity of the axons of the cells (Cleland, Dubin & Levick, 1971; Fukuda, 1971; Hoffmann, Stone & Sherman, 1972; Ikeda & Wright, 1972; Cleland, Levick & Sanderson, 1973; Cleland & Levick, 1974*a*; Stone & Fukuda, 1974). A further distinction between cells with very slow conduction velocities (W cells) and cells with moderate and fast conduction velocities (X and Y cells) has also been made in the cat, and this also correlates with certain receptive field properties (Stone & Hoffmann, 1972; Hoffman, 1973; Cleland & Levick, 1974*a*, *b*; Stone & Fukuda, 1974).

Our prime aim in undertaking this study was to complete the description of the centre surround receptive fields in the rabbit as a control for studies on the effects of picrotoxin and strychnine on the various types of receptive field (Caldwell, Daw & Wyatt, 1978; Caldwell & Daw, 1978). In the course of the studies it became apparent that some of the correlations suggested in the cat between conduction velocity, spontaneous activity and receptive field properties might not hold for all retinas, so we decided to accumulate data on those points as well.

METHODS

Preparation for recording. The procedures were much the same as those described previously for recording from rabbit retinas (Barlow *et al.* 1964; Daw & Wyatt, 1974). Adult pigmented rabbits, weighing 2–3 kg, were anaesthetized with 1–4% fluothane in 70% O_2/30% N_2O. The fluothane was discontinued after surgery and anaesthesia maintained with N_2O. All wounds were infiltrated with a local anaesthetic. The animal was paralysed after surgery with an I.M. injection of D-tubocurarine (initial and maintenance dose of 0·5 mg/kg.hr). It was held with ear bars and a chin bar and respired via a tracheal cannula. Expiratory CO_2 was measured with a Beckman gas analyser and was maintained between 3·5 and 5%. A catheter in the femoral

artery monitored blood pressure. Body temperature, measured with a rectal thermometer, was kept at 37–40 °C with a heating pad.

Contact lenses protected the cornea, and the pupil was dilated with atropine sulphate. The contact lenses were chosen to focus the tangent screen upon the retina; when necessary, additional spectacle lenses were used. Focus was checked with a retinoscope. The projection of the optic nerve head, retinal blood vessels, and medullary ray border were plotted on the tangent screen with an ophthalmoscope and corner cube. The screen was 75 cm from the eye.

The recording was intraocular, with the electrode inserted through the sclera. Electrode position was observed with an ophthalmoscope. The electrode tip was placed beneath the optic nerve head and approximately 3° below the border of the medullary rays. Thus recordings from cell bodies were made in the visual streak. The electrode also recorded from axons whose receptive fields were located in the more inferior retina. The electrodes were tungsten-in-glass (Levick, 1972).

Signals from the electrode went to standard amplification and display equipment. A LINC computer was used to collect a peristimulus time histogram with 500 bins. A variable time could be chosen for the bin size. With stationary stimuli the first 100 bins were prestimulus; the stimulus was on during bins 101 to 300; bins 301 to 500 were post-stimulus. With moving stimuli the histogram was begun when the stimulus crossed a pin diode placed in the path of the stimulus. All histograms shown are for four repetitions of the stimulus. A typical bin width was 10 msec, for a histogram 5 sec long. In this case 10 spikes/bin for the histogram represented an average of 2·5 spikes/10 msec in each repetition of the stimulus, or 250 spikes/sec. This conversion has been made in each case so that the calibrations are given in average spikes/sec for a single presentation of the stimulus.

Bipolar electrodes were inserted through the skull to the optic chiasm for antidromic stimulation of ganglion cells. The stimuli were generally 50 μsec duration and 1–100 V amplitude. In several experiments the brain was dissected away after completion of the recordings, and the distance from the electrodes to the eye was measured; this distance was 13 mm in most animals.

Visual stimulation. Light and dark objects such as spots, bars, and annuli were projected onto a tangent screen. A trapezoid generator, controlling a mirror mounted on a penmotor, was used to move the image across the screen (speeds from 0·3 to 380°/sec in any direction). A 'noise board' with a variety of shapes was often used while searching for units since most centre surround sluggish cells, local edge detectors, and 'on' direction selective cells did not respond to diffuse light and had little or no spontaneous activity. Most experiments were performed at mesopic light levels with a background of about 1 cd/m^2. Stimuli were usually 3–10 cd/m^2.

The classification of X and Y cells requires a variety of tests. They were originally distinguished by the linearity or nonlinearity of summation over the receptive field (Enroch-Cugell & Robson, 1966). For this test we flickered light sinusoidally between one half of the receptive field and the other by means of two pieces of Polaroid filter side by side in the projector, and another rotating in front of the projector. The rate of flicker and the area of receptive field illuminated were adjusted to get the best response from the cell being recorded. The split field was then moved laterally, to see if there was a position of the boundary within the receptive field centre at which the response to the flicker would disappear. For this test, the stimulus was less than 0·5 log units above background.

Other tests which we used and parameters which we measured were (i) the response to a spot of light covering the centre of the receptive field, an annulus covering the periphery, and diffuse illumination covering the whole receptive field; (ii) the responses to a series of gratings of various spatial frequencies, moved across the receptive field with a velocity inversely proportional to the spatial frequency, so that two edges crossed the field per second (Enroth-Cugell & Robson, 1966); (iii) a disk, white on one side and black on the other, rotated about its diameter in the centre of the receptive field (Cleland & Levick, 1974*a*); (iv) the response to a radial grating, centred on the receptive field but masked from the centre of the receptive field so that it only illuminated the surround. Also, comparison of the response to a spot of light in the centre of the receptive field with such a grating stationary and with such a grating rotating (Werblin, 1972; Cleland *et al.* 1973; Werblin & Copenhagen, 1974; Cleland & Levick, 1974*a*); (v) the variation of response with speed for black and white spots moved across the receptive field (Cleland *et al.* 1971); (vi) the response to black and white objects moved into and out of the receptive field; (vii) the response to stimuli of various wave-lengths; (viii) the spontaneous activity and its regularity.

Two possible ways to evaluate a cell's response to movement are the maximum frequency of firing during the response and the average rate of firing during the response. One or both of these may be important signals to the post-synaptic cell. We have chosen to use the average frequency of firing which is determined by the total number of action potentials in the response divided by the total time of the response. In several cases the maximum frequency of firing was also plotted and had the same shape and optimal speed as did the average frequency plot.

RESULTS

The principal new finding is that centre surround cells in the rabbit can be separated into subclasses very similar to those reported in the cat (Enroth-Cugell & Robson, 1966; Cleland & Levick, 1974*a*; Stone & Fukuda, 1974). In the present study these cells have been separated into eight categories like those in the cat and a ninth

TABLE 1. Receptive field types

	Present experiments (streak and periphery)			Oyster (1968), periphery	Levick (1967), streak
Concentric	%	No.		(%)	(%)
Y					
On	10.6	(65)			
Off	18·7	(115)			
X					
On (11 colour coded)	5·4	(33)			
Off	3·4	(21)	on 23·7 %	25·9	16·2
Sluggish transient			off 27·0 %	33·7	25·3
On	4·9	(30)			
Off	4·4	(27)			
Sluggish sustained					
On	2·8	(17)			
Off	0·5	(3)			
Direction selective					
On-off	25·7	(158)		20·6	10·4
On	3·4	(21)		5·0	7·1
Orientation selective	6·7	(41)		1·1	11·0
Local edge detector	4·7	(29)		3·0	19·5
Large field	2·6	(16)		6·3	4·6
Uniformity	0·7	(4)		1·4	2·6
Hybrid	2·6	(16)			
Unclassified	2·9	(18)		3·0	3·3
Total	100	(614)		100	100

In early experiments large field cells were not carefully distinguished; some cells classified as Y were probably large field. Colour coding was not tested in early experiments. Ten of the last twelve on X cells were colour coded, suggesting that the percentage of on X cells which are colour coded may be quite high. The unclassified category includes only those cells whose receptive fields could be located and plotted.

hybrid category. Another centre surround type is colour coded. The classification is based on a study of 614 units which includes recordings from axons of cells located inferior to the streak as well as cell bodies near the centre of the visual streak (see Table 1).

A brief comment is necessary about the nomenclature used here in relation to those used in the cat. The tests used in the present experiments include those of Cleland

& Levick (1974*a*), who used the terms brisk versus sluggish and transient versus sustained. They concluded that the brisk, transient cells and brisk, sustained cells were very nearly equivalent to the Y and X types, respectively, of Enroth-Cugell & Robson (1966). However, ganglion cells in the cat cannot be classified as X or Y simply on the basis of the transient or sustained nature of their response. This is also true in the rabbit where many cells have both transient and sustained components in their response. Therefore, we have used the X/Y notation which does not imply a particular response to stationary contrast. The W category was originally set up to include all those cells with slowly conducting axons, both centre surround and complex (Stone & Hoffman, 1972; Stone & Fukuda, 1974). This is a heterogeneous group in terms of receptive field properties and also heterogeneous in the rabbit in terms of conduction velocity. Consequently we will refer to the centre surround cells with slowly conducting axons as sluggish centre surround cells, and the cells with more complex receptive fields by their descriptive names – direction selective, orientation selective, uniformity detectors and large field units. The resulting nomenclature is schizophrenic, but has the merit that it avoids some of the problems that both the Cleland & Levick and Stone nomenclatures have, and at the same time emphasizes those respects in which cat and rabbit retinas are similar.

Centre surround cells: distinction of sluggish cells from brisk cells (X and Y)

Sluggish centre surround cells in the rabbit are clearly separate from X and Y (brisk) cells and are the easiest of these types to identify. They respond only to relatively slowly moving objects (Fig. 1) and have slowly conducting axons (Fig. 2). They usually had spontaneous activity much less than 1/sec. These three characteristics correlated with each other and identified a sluggish centre surround cell almost unequivocally. Other qualities and tests were also correlated. The maximum frequency of firing in response to a stimulus was usually less than for X or Y cells. The response to a twirling disk occurred only if the disk was barely rotating. Sluggish cells generally did not respond to moving vertical gratings at the speeds normally used for X and Y cells ($\sim$ 1 c/sec); a few sluggish cells would respond to the grating if it was moved very slowly but most did not even respond to this. This lack of a response with moving gratings indicated a strong suppressive surround as found with sluggish centre surround cells in the cat retina.

Sluggish cells could be subdivided into sustained and transient classes. Although a stationary contrast stimulus was not very useful in separating sluggish from brisk (X and Y) cells (Fig. 3), it was often used to separate sustained from transient sluggish cells. Transient sluggish centre surround cells rarely had any sustained response. There were other differences between sustained and transient sluggish cells. Only the transient sluggish cells were severely inhibited by a rotating radial grating. Only a subset of the transient sluggish cells responded well to moving vertical gratings. All transient sluggish cells responded equally well to black versus white objects (moving or stationary) but some sustained sluggish cells had asymmetric responses: on centre sustained sluggish cells often responded poorly to a small black object and off centre sustained sluggish cells responded poorly to white spots. This asymmetry of the response may have been the reason that so few off centre sustained sluggish cells were found in this study (Table 1) since white spots were often used to

search for the receptive field (see Cleland & Levick, 1974*a*). The question of whether sustained sluggish cells are linear and transient sluggish cells are non-linear is largely moot, since most sluggish cells do not respond at all to the stimuli traditionally

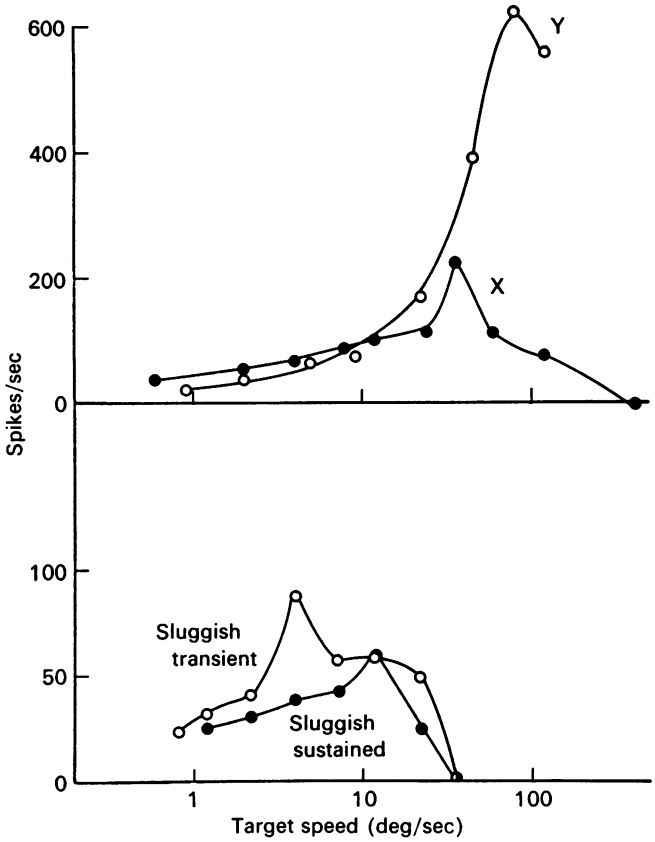

Fig. 1. Sensitivity to movement. Comparison of X, Y, sluggish sustained and sluggish transient cells. Each curve is of a single cell which is a representative example. Average frequency of firing is plotted versus target speed. Both X and Y cells respond to higher speeds than sluggish cells and the frequency of firing of X and Y cells is greater than that of sluggish cells.

used to classify centre surround cells with fast conduction velocities into linear (X) and non-linear (Y). Thus in the rabbit the four types of centre surround sluggish cells (sustained and transient with on or off centres) are relatively easy to classify by the same tests used in the cat.

Separation of X and Y cells

The distinction of X and Y cells in the cat is usually based on the linearity tests of Enroth-Cugell & Robson (1966). In the rabbit, as in the cat, we found that some tests were well correlated with these linearity tests, and others were not. The tests which were the strongest indicators of X or Y cells were moving vertical gratings, a linearity test, and movement of a large object of contrast optimal for stimulating the

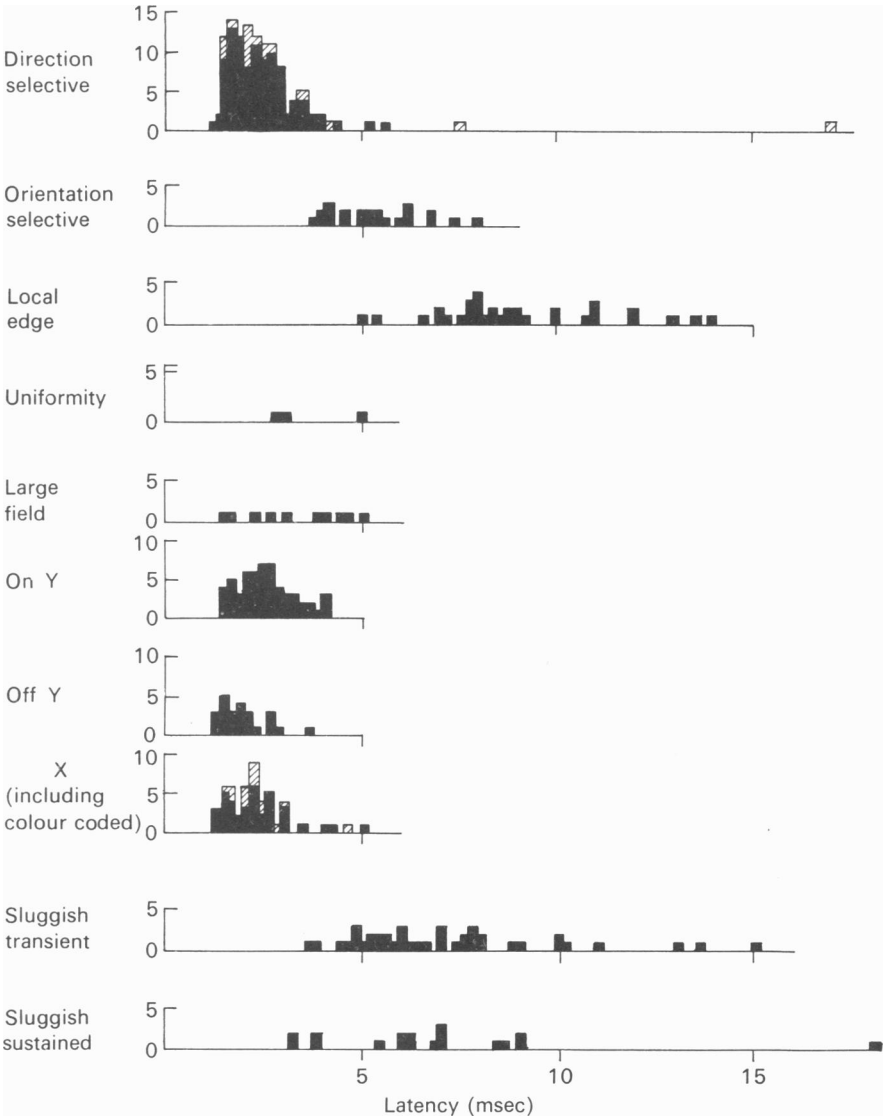

Fig. 2. Conduction latency from antidromic stimulation at the optic chiasm. Cells in the upper half of the figure have complex receptive fields; X, Y and sluggish cells have centre surround receptive fields. Both types of direction selective cells have rapidly conducting axons (on direction selective units are hatched bars and the on–off units are solid bars). Large field cells also have moderately fast conducting axons. Conduction latencies of X and Y cells were largely overlapping with each other but not with sluggish centre surround cells. Almost all sluggish cells had latencies longer than 4 msec. Those X cells that were shown to be colour coded are hatched.

surround. Tests which were sometimes useful were stationary contrast (spot and annulus) and a rotating radial grating. The rate and regularity of spontaneous activity was also sometimes a good indicator. Two tests for separating X and Y cells which are correlated with the Enroth-Cugell & Robson tests in the cat but which are not in the rabbit were the antidromic latency from electrical stimulation at the optic chiasm and the periphery effect. All of these tests are described below.

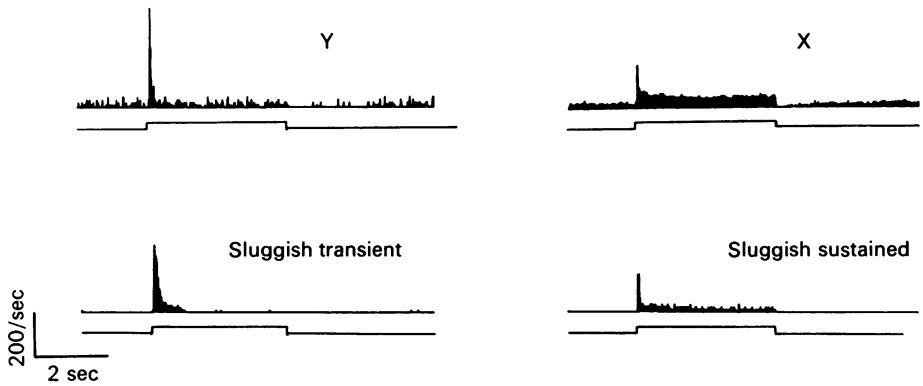

Fig. 3. Response to a stationary white spot in the centre of the receptive field. Peristimulus time histograms. The initial section of each record is prestimulus. The spot was on while the trace beneath the histograms was shifted upward. The last part of the record is post-stimulus. All cells were on centre. Both the Y cell and the sluggish transient cell had very transient responses, but the Y cell had a higher maximum frequency of firing and more spontaneous activity than the sluggish cell. The X cell had a higher and more regular spontaneous activity than either the Y cell or the sluggish sustained cell.

Moving vertical gratings divided cells into two groups in the rabbit just as in the cat. Maximum spatial frequency was not studied quantitatively, but X and Y cells in the rabbit responded to increasing spatial frequency just as X and Y (Enroth-Cugell & Robson, 1966) and sustained and transient (Cleland *et al.* 1971) cells do in the cat. As the spatial frequency increased, a transition occurred from a modulated response at lower frequencies to either no response (X cells) or unmodulated firing during movement (Y cells).

A stimulus which tested the ability of a cell to sum light linearly in different areas of the receptive field was the original basis of classifying X and Y cells. The linearity test (see Methods) used in the present experiments defined X and Y cells in much the same way as in the cat: for X cells a position in the receptive field could be found at which the stimulus had no effect on the cell, but for Y cells there was no 'null' position, and when the stimulus was centred over the receptive field of a Y cell it usually responded at twice the modulation frequency which was between 1 and 4 Hz. Hochstein & Shapley (1976) have used this Y cell property, namely the generation of the second order harmonic, to separate X and Y cells in the cat in a more rigorous way.

A test designed to stimulate the receptive field surround with a moving target was used by Cleland *et al.* (1971). For example, to stimulate an on centre cell, the target was a large black object. Cells classified as Y cells would respond to extremely fast

speeds (several hundred degrees/sec) with a high frequency burst. X cells would not respond as well to these high speeds. The same was true in the rabbit. Although Y cells tended to respond better than X cells to movement of a small spot (Fig. 1), fast movement of a *small* spot was not sufficient to classify the cells.

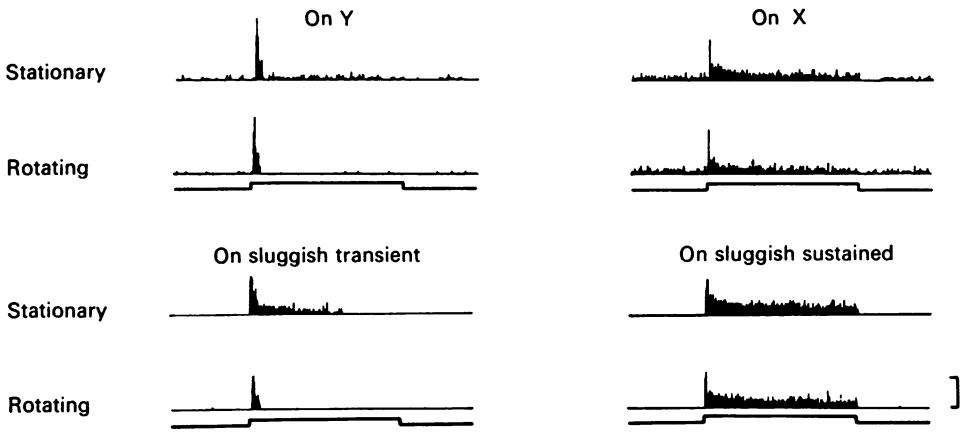

Fig. 4. Inhibition of the response to a central spot by rotation of a radial grating. The spot was on while the trace beneath the histogram was shifted upward. The grating was on continuously and either stationary during the entire histogram or rotating during the entire programme. Spot size rather smaller than the centre of the receptive field. Grating masked from an area rather larger than the centre of the receptive field. 24 sectors to the grating. There is a large effect of rotation upon the sluggish transient cell and some effect upon the Y cell; the small sustained component was eliminated by rotation of the grating and the transient slightly reduced. Y and sluggish transient cells: calibration scale is 250 spikes/sec and the light was on 2 sec. X and sluggish sustained cells: calibration scale is 125 spikes/sec and the light was on 4 sec.

The response to a stationary spot or annulus was sometimes correlated with these tests. Transient responses can be misleading for technical reasons, but when all the necessary precautions are taken, it would still be difficult to base a classification in the rabbit upon the response to stationary contrast because many cells have both transient and sustained responses. A cell which had a purely transient response was usually a Y cell by all other criteria. Other cells, particularly the colour coded cells, had especially sustained responses and were X cells by all other criteria. Nevertheless, it is an oversimplification to consider X cells as sustained and Y cells as transient (Jakiela, Enroth-Cugell, & Shapley, 1976). Neither a recent study on cat ganglion cells (Cleland & Levick, 1974*a*) nor the original description of X and Y cells (Enroth-Cugell & Robson, 1966) used this transient/sustained test as the most important feature (however, see Fukuda, 1971; Ikeda and Wright, 1972).

Previous results suggest that rotation of a radial grating affects Y cells in the cat in two ways, but has much less affect on X cells (Cleland *et al.* 1973; Cleland & Levick, 1974*a*). One effect is that rotation of the grating increases the steady discharge of the cell. The other concerns the effect of the grating upon the response to a spot flashed in the centre of the receptive field: the response to such a spot is reduced when the grating is rotated compared to when it is stationary. The effects in the

rabbit were more complex in two respects: first, a greater variety of effects was obtained and second, the distinction betwen X and Y cells was not so clear. For many Y cells, rotation of the grating reduced the activity of the cell. This is reminiscent of Y cells in the cat geniculate rather than the retina (Levick, Cleland & Dubin, 1972). Some Y cells were excited by the grating, as in the cat retina, and some were unaffected by it. Nearly all X cells were unaffected by rotation of the grating itself. The response to a spot in the centre of the receptive field was inhibited by rotation of the grating for many Y cells (Fig. 4), both on centre and off centre, but this was also true for some off centre cells classified as X by the previous criteria. Consequently the radial grating effects were good for on centre cells but not for off centre cells as an X/Y criterion. It may be that the effects of rotating gratings in the cat are also more complicated than has previously been suggested (H. G. Jakiela, R. Shapley & C. Enroth-Cugell, private communication).

The rate of spontaneous activity was somewhat correlated with the X or Y classification. X cells tended to have a higher and more regular rate of spontaneous activity, although the spontaneous activity was not as high as that in the cat. The maximum spontaneous activity of X cells in the rabbit was about 30/sec compared to 40–80/sec in the cat (Stone & Fukuda, 1974). It is unlikely that this could be due to different levels of background brightness because Stone & Fukuda (1974) show that the rate of spontaneous activity is unaffected by the background brightness for almost all centre surround cell types.

Two tests which separate X and Y cells in the cat were found to be almost useless for the rabbit. These were the antidromic conduction latency and the periphery effect. The conduction latencies of X and Y cells in the cat do not overlap. In the rabbit, however, there was essentially complete overlap (Fig. 2) of the latencies of X and Y cells (identified by the other tests). Of course, latency to stimulation at the optic chiasm and conduction velocity are different things. Unfortunately, a good estimate of the conduction velocity cannot be made from these experiments since the cells were stimulated electrically at only one position. It is possible that X and Y cells in the rabbit do have different conduction velocities but that the difference was not observed in the present experiments for reasons that are peculiar to the rabbit or the position of the recording electrode (see Discussion). One technical possibility that can be excluded is that a difference in latencies was obscured by placement of the recording electrode in different regions of the retina. The electrode was nearly always placed in the approximate centre of the visual streak, directly inferior to the optic nerve head.

The periphery effect (McIlwain, 1964) was a second test in which the distinction between X and Y cells in the rabbit was not as clear as in the cat. A strong periphery effect can only be easily demonstrated in the cat for brisk, transient (Y), not brisk, sustained (X) cells (Cleland *et al.* 1973). There was never a clear example of a periphery effect in the rabbit for any of the X or Y cells which were tested in the early experiments, consequently the test was dropped in the later experiments.

In general, it appears to be harder to distinguish X cells from Y cells in the rabbit than in the cat. We found that the responses to moving vertical gratings and movement of an object designed to stimulate the surround were well correlated with the linearity test on which the distinction was originally made. In future work the results

from any one of these tests could probably be used as a criterion; these are also the tests that are best correlated with each other in the cat (Hochstein & Shapley, 1976). An extremely transient or sustained response, or some aspects of the response to a radial grating were also well correlated with the results of these three tests, and could sometimes be used to make a classification. Although the rate of spontaneous activity was also correlated with the results of the other tests, it is unlikely that it could ever be used by itself to classify a cell. In any case, it would seem wise to continue to use all of these tests in order to be certain of one's classification.

Pigments involved in rabbit vision

Over eighty-five cells of various types other than colour coded were tested for an indication of their spectral sensitivity at various levels of background luminance. Threshold was compared for 420 nm and for 590 nm stimuli which were calculated

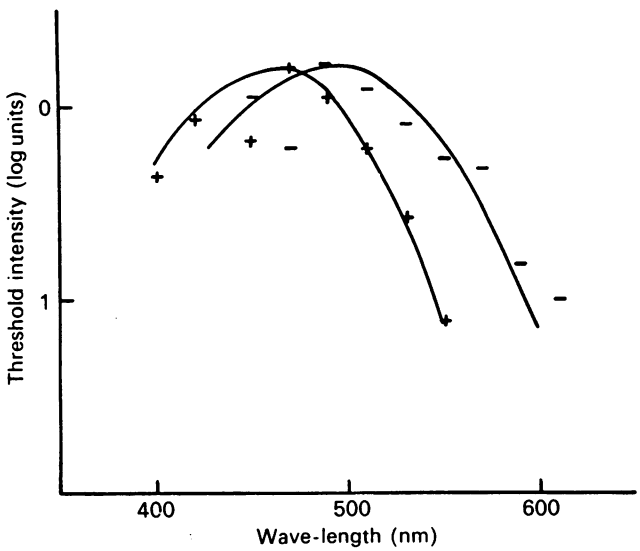

Fig. 5. Spectral sensitivities for an on centre X colour unit against coloured backgrounds. Plusses are thresholds for on responses to a spot in the centre of the receptive field against a green background (Baird Atomic 570 nm interference filter). The curve is the Dartnall nomogram for a pigment with a peak at 465 nm. Minuses are the thresholds for the off responses to an annulus against a blue background (Baird Atomic 420 nm interference filter). The curve that closely fits these points is the Dartnall nomogram for a pigment that peaks at 500 nm.

to be equivalent stimuli for a 500 nm rod pigment. We found no evidence for a pigment with a spectral sensitivity much different from the rods, even at levels that are high mesopic and low photopic for cat and human (2000 td). The data showed that these cells had no input from cones with pigments peaking at less than 500 nm or greater than 520 nm. Whenever tested, the cells responded at a photopic level. Assuming that rods in the rabbit saturate at the same levels as those in the cat (Daw & Pearlman, 1969) and rods in the human (Aguilar & Stiles, 1954) there must be

a cone input with connexions which are equivalent to the rod input, and a spectral sensitivity very close to the rods.

Colour coding. Ten of the last twelve on centre X cells recorded in these experiments were colour coded. This is probably closer to the true percentage of on centre X cells which are colour coded than the percentage shown in Table 1, because many of the on centre X cells in the early experiments were not tested for colour coding. The on centre X cell was the only type of ganglion cell which was found to be colour coded. These cells had short conduction latencies and were X cells by all criteria. The spatial organization was similar to the colour coded cells in the cat retina (Cleland & Levick, 1974*b*; Rowe & Stone, 1976); they were blue-on and sometimes also green-on in the centre with a green-off surround. The different colour components were difficult to isolate in the rabbit even with monochromatic adapating backgrounds because of the closeness of the peaks of the pigment curves. The spectral sensitivities of the blue centre and green surround from one unit are shown in Fig. 5. The blue pigment is best fitted by a 465 nm pigment curve and the green by a 500 nm pigment curve, but the deviance of some points from the curves suggests that more measurements will be necessary to define these peaks carefully.

Colour coding was retained at both mesopic and photopic levels. This is reasonable if there are green cones which have the same effect as rods on the ganglion cell, as suggested by the lack of a Purkinje shift in non-colour coded cells.

The colour coded units were equally distributed between the streak and the periphery, a finding that agrees with the statement of Hughes (1971) that the percentage of receptors which are cones is the same in the streak and inferior peripheral retina. It also suggests that the percentage of cones peaking at 450–470 nm as opposed to 500–520 nm is constant in the streak and inferior retina, although the number of colour-coded units that have been recorded so far is not large enough to make this a strong statement.

Ganglion cells with more complex receptive fields

Ganglion cells with more complex receptive fields have already been carefully studied in the rabbit (Barlow *et al.* 1964; Levick, 1967). Some new information about complex cell properties is presented here, primarily the conduction latency for several examples of each class of cell. The most interesting finding was the antidromic conduction latencies of direction selective cells. In contrast to the slowly conducting direction selective cells in the cat retina (Cleland & Levick, 1974*b*; Stone & Fukuda, 1974), both the 'on-off' and the 'on' direction selective cells of the rabbit have moderately rapid conducting axons (Fig. 2). Thus neither type of direction selective cell would fit into the W cell category proposed by Stone & Fukuda (1974) for the cat, and in the rabbit one cannot make the generalization that cells with complex receptive fields have slowly conducting axons.

The 'on' direction selective cells seem to be an exception to another general rule. This is the generalization that cells with a sluggish response have slowly conducting axons, and cells with a brisk response have fast conducting axons. Even though the 'on' directionally selective cells seem very much like centre surround sluggish cells in having low spontaneous activity and responding only to low target speeds, their conduction latencies ranged from 1·5 to 4·0 msec (excluding one latency of 7·5 msec

and one of 17 msec) with a mean of 2·4 msec (n = 15). This overlaps the values recorded from X and Y cells considerably, and is very different from the values recorded from centre surround sluggish cells (Fig. 2).

There have been no descriptions for the rabbit of the responsiveness of 'on' directionally selective cells to an annulus. Many centre surround ganglion cells, especially W cells, have concentric surrounds which are only evident with an annulus which stimulates the entire surround. Stone & Fukuda (1974) reported that 'on'

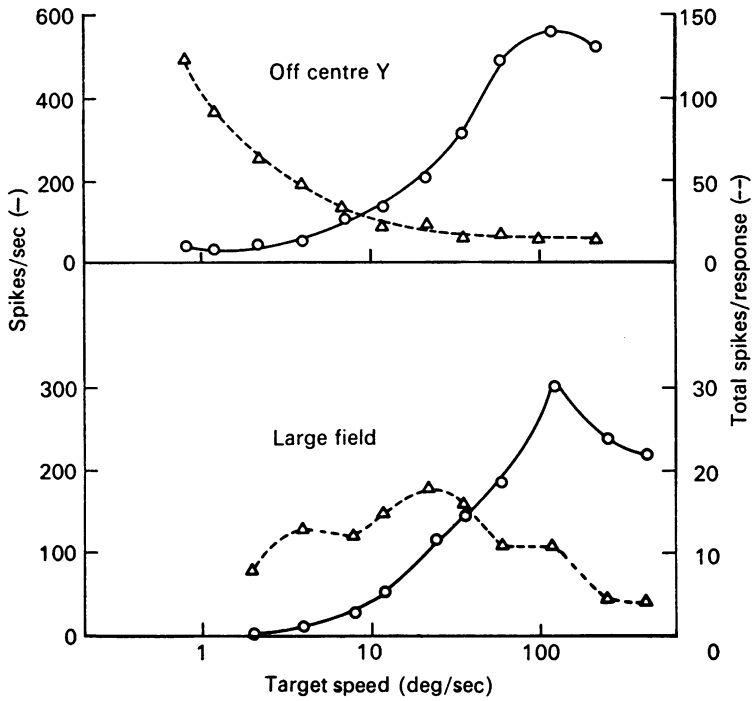

Fig. 6. Comparison of the responses to movement for an off centre Y cell and a large field cell. At slow speeds the total number of action potentials (dashed line through the triangles) of the large field cell is much less than that of the off Y cell even though both cells have similar response in terms of the frequency of firing (continuous line through the open circles). Note the difference in scales.

directionally sensitive cells in the cat have a surround that may cause excitation as well as inhibition; these cells, unlike 'on-off' direction selective cells, are excited at the offset of an annulus. The same was true for three 'on' directionally selective cells tested with an annulus in these experiments: in each case the annulus inhibited the centre response and gave an 'off' response. This correlates with the fact that 'on' directionally sensitive cells are more responsive to small objects than large ones (Wyatt & Daw, 1975, 1976).

As noted by Oyster (1968), large field cells are easily confused with certain centre surround cells (specifically cells classified here as Y). The number of large field cells is under represented in Table 1 and Fig. 2 because this distinction was not carefully made in the early experiments. Although the conduction latencies of the large field

and Y cells overlap, the large field cells tended to have longer latencies. The difference in the response to a moving target is a clear distinction between the large field and Y cells (Fig. 6). Large field cells respond poorly to slow targets, as was noted by Barlow *et al.* (1964). As the target speed decreases the total number of action potentials is often constant or decreases for the large field cell but increases rapidly for the Y cell.

The receptive field properties of the orientation selective, local edge detector, and uniformity cells have already been described by Levick (1967) and we have nothing new to add with respect to the visual responses. We measured the conduction latencies of these cells and both the orientation selective and local edge detector cells have slowly conducting axons with latencies which overlap those of the centre surround sluggish cells (Fig. 2). Only three conduction latencies were measured for the uniformity cells: it will be necessary to accumulate a larger sample before one can determine whether the latencies overlap the X, Y and directionally sensitive group or the orientation selective, local edge and centre surround sluggish group.

Unclassified cells and hybrid units

In our sample of 614 units, 580 (95 %) could be classified into one of the previously described centre surround types or one of the six more complex types. In the case of the centre surround types, this meant that at least three tests, and usually more than that, correlated with each other to give the classification. For the other thirty-four units (5·5 %), the situation was not so clear. In some cases the results of the tests were ambiguous. Eighteen units (2·9 %) were categorized as unclassified for these reasons.

Sixteen cells (2·6 %) with centre surround receptive fields, however, produced unambiguous evidence that they should be classified as sluggish by receptive field tests and as brisk (X or Y) by conduction velocity. These cells had surrounds which were strongly affected by picrotoxin (Caldwell & Daw, 1978), unlike other centre surround types and therefore deserve separate mention. The cells were all on centre with sustained responses. Their conduction latencies averaged $2{\cdot}4 \pm 0.6$ msec. They responded only to slow speeds of movement, gave a poor response to a twirling disk, and had low spontaneous activity, which are all properties of sluggish centre surround cells. Movement of a radial grating had some effect, which is unusual for an on centre cell with a sustained response. Where it was tested, they were not colour coded. The linearity test was ambiguous. These properties are reminiscent of 'on' directionally selective cells, and in two cases there was some asymmetry in the response to movement, but not enough to classify the cell as directionally sensitive, and certainly no suggestion of a null direction. The cells could be described as like on sustained sluggish cells in terms of their receptive field properties, except for the radial grating effect, like on X cells in terms of their conduction velocity, and most of all like 'on' directionally sensitive cells without the directional sensitivity. We decided to call these cells hybrid units, to imply that they have features of both sluggish cells and brisk (X or Y) cells.

DISCUSSION

The most important result of this study is the similarity between the types of centre surround receptive field found in cat, rabbit and other retinas. The presence of transient and sustained centre surround cells in the rabbit had been noted before (Hughes, 1971; Oyster, Takahashi & Levick, 1971) but the correspondence between these cells and the X and Y cells of the cat was not studied in detail. There is evidence of X and Y cells in the tree shrew (Sherman, Norton, & Casagrande, 1975) and owl monkey (Sherman, Wilson, Kaas & Webb, 1976), but there is little information about the general occurrence of W-like cells. The existence of W-like cells has been proposed from measurements of conduction velocity and soma size in the rat (Fukuda, 1977); and receptive field properties and conduction velocity in the possum (M. H. Rowe, E. Tancred, B. Freeman & J. Stone, private communication). Sustained, transient and slowly conducting fibres are also found in the monkey (De Monasterio & Gouras, 1975; Schiller & Malpeli, 1977). In the present experiments the subdivision of centre surround cells in the cat has been found to be valid also in the rabbit. There are eight subclasses: X, Y, sluggish sustained and sluggish transient, all of which can be either on centre or off centre. The general existence of sluggish and slowly conducting cells is especially significant in view of the evidence from the cat optic nerve conduction velocities and fibre sizes (Bishop, Clare & Landau, 1969; Hughes & Wässle, 1976) and from the distribution of soma sizes in the cat (Boycott & Wässle, 1974; Fukuda & Stone, 1974; Rowe & Stone, 1976) that the W cell category may include a large percentage of the ganglion cells.

One striking point in our experiments was that it was much easier to distinguish centre surround sluggish cells from brisk (X and Y) cells, than X cells from Y cells. Spontaneous activity, speed specificity, conduction velocity and size specificity could each be used to make the brisk/sluggish distinction much more clearly than the X/Y distinction. One test usually sufficed for the first distinction, whereas several were often necessary for the second. Cats and rabbits are not often faced with drifting or alternating gratings in the real world, or the niceties that have crept into controversies about X and Y cells, so it may turn out, from the functional point of view, that the brisk/sluggish distinction is a much more important one than the X/Y distinction.

It was unfortunate that there was considerable overlap in conduction latency between X and Y cells, because this is an easily measured parameter and is highly correlated with other properties of X and Y cells in the cat. It is possible that the conduction velocities of X and Y cells in the rabbit are not overlapping even though the latencies measured from antidromic stimulation did overlap. One factor that might obscure a possible difference in X and Y latencies is the unusual myelination of the axons; in the cat myelination occurs as the fibres leave the eye but in the rabbit the fibres myelinate within the retina in a band termed the medullary rays. The centre of the visual streak is close to the border of this band of myelinated fibres. Granit & Marg (1958) state that individual axons myelinate randomly within the band, which extends about 2 mm beneath the optic nerve head. From other observations, we found that the maximum intraretinal conduction velocity of unmyelinated axons in the rabbit is about 1–2 m/sec. Since the fastest myelinated axons (X and Y) have a conduction velocity of 25–50 m/sec (Granit & Marg, 1958), most of the latency

measured in these experiments must be intraretinal. Thus it is quite possible that the random initiation of myelination in conjunction with recording close to the band of myelination has blurred a difference in the conduction speed of X and Y cells. It is even possible that Y cells consistently myelinate closer to the optic disk.

The existence of the hybrid cells, which were like 'on' directionally sensitive cells without the directional sensitivity, will be taken up in a later paper, because of the dramatic effects of picrotoxin on them (Caldwell & Daw, 1978). Rowe & Stone (1976) suggested that in the cat retina there is a continuum between direction selective and non direction selective cells. Their discussion concerned 'on–off' direction selective cells, and we have seen no hint of a continuum between direction sensitivity and no direction sensitivity for 'on–off' cells in the rabbit. Actually, the only 'on–off' cells in the rabbit besides the direction sensitive ones are the local edge detectors, and their properties are different in many respects. However, there may be a continuum between the hybrid units and the 'on' direction sensitive cells in the rabbit. We do not believe that the hybrid units were damaged cells, because some of them were recorded as fibres.

Ganglion cells in the cat with more complex receptive fields (Cleland & Levick, 1974; Stone & Fukuda, 1974; Rowe & Stone, 1976) are also similar to those in the rabbit. There are some exceptions: large field cells have not been described in the cat retina and the off centre edge inhibitory cells which are found in the cat have not been found in the rabbit. Yet all of the other complex cells are found in both animals and even colour coded cells are similarly organized, with short wave-lengths excitatory to the centre and longer wave-lengths providing the surround. The main difference between the two animals, with respect to cells with more complex receptive fields, is that directionally sensitive cells have slow conduction velocities in the cat and fast ones in the rabbit. If the conduction velocity of the axon is an indication of the size of the cell soma, it is likely that the somas of both types of direction selective cells are among the larger ganglion cells in the rabbit. Thus the high probability of recording from these cells in the rabbit as compared to the cat could be related to the soma size rather than to a difference in the true percentage of directional cells in the retina.

There are functional reasons why both types of directionally sensitive cells in the rabbit retina should have fast conduction velocities. The 'on' directionally sensitive cells may well be involved in reflex eye movement control (Oyster, 1968; Oyster, Takahashi & Collewijn, 1972). Long latencies are to be avoided in this system, if accurate tracking is to be achieved. The 'on–off' directionally sensitive cells may be involved in eye movement control or in detecting the approach of hawks and other predators, with rapid escape being a matter of life and death. Movement detection in higher mammals is very likely based on neural networks at higher levels, with input from the fast conducting X and Y cells.

The question of colour coding and visual pigments in the rabbit has yet to be fully answered. Sjöstrand & Nilsson (1964) decided from electron micrographs that there were only rods, typical and atypical, but Hughes (1971) argues that the atypical rods are actually cones when one considers the morphology of the base or pedicle of the receptor. There is physiological evidence that the rabbit has two types of receptors and it seems reasonable to assume that they can see on a bright day in a photopic

situation. Dodt & Elenius (1960) used the amplitude of the ERG b wave for a criterion response and measured the change of threshold during dark adaptation. The adaptation curve had a break in it, suggesting that the rabbit has both scotopic and photopic vision. By measuring the dark adaptation curve with orange and blue light at different background levels they showed the lack of a Purkinje effect. This suggests that there is a cone pigment with the same spectral sensitivity as the rod pigment. In agreement with this is the fact that no sign of a Purkinje shift was found in the present experiments on single units. Dodt & Walther (1958) used a rapidly flickering stimulus to isolate the cone responses and measured spectral sensitivities. They found a maximum sensitivity at 500 nm, again implying a cone pigment near 500 nm. Conner & MacLeod (1977), however, have recently suggested that rods will respond to high flicker rates, which would make the evidence of Dodt and Walther ambiguous.

Hill (1962) and Hill & Marg (1963) found evidence of colour coding in the higher visual centres of the rabbit. In the lateral geniculate Hill found both excitation and inhibition to the onset of blue light. This suggests either that some ganglion cells which are inhibited by blue light have been missed in the present study or that the colour coded on centre X cells are both excitatory and inhibitory in the lateral geniculate. Hill & Marg found excitation and inhibition to the onset of blue light in the transpeduncular nucleus; the maximum sensitivity of the blue was 460 nm.

Nuboer (1971) has evidence from behavioural experiments that the rabbit has a blue and green system in addition to the rods. He has evidence both for and against a green pigment with a peak sensitivity at 530 nm.

The present experiments suggest that the rabbit has not only rods and cones with pigments of similar spectral sensitivity but also receptors with a blue pigment of maximal sensitivity near 465 nm. These conclusions are based on the lack of a Purkinje shift and on the properties of colour coded ganglion cells with a blue-on centre and a green antagonistic surround. This agrees in general with De Monasterio's results from intracellular recordings in ganglion cells, but his results define the spectral sensitivities more carefully and suggest that the spectral sensitivities of the cones peak at 430 and 520 nm (private communication). The fact that his recordings were made with an eye cup without the lens on might account for part of the discrepancy between the spectral sensitivities measured by him and us for the blue cone pigment.

It is now possible to identify at least fifteen physiologically different ganglion cells in the rabbit retina and an almost equally large number of similar cells in the cat retina. The distinction between ganglion cell receptive field types in the rabbit is usually quite obvious. For example, the only cells with 'on–off' receptive fields are the 'on–off' direction selective and the local edge detector cells and there is never any confusion of one with the other. How this information is processed by the animal is a further question. In the cat X cells have central projections to the lateral geniculate nucleus (layers A, A_1 and C) and to the mid-brain (but not the superior colliculus), Y cells project to both the lateral geniculate nucleus and the superior colliculus, and W cells project to the superior colliculus and only to laminas C, C_1 and C_2 (parvocellular layers) of the lateral geniculate (Cleland *et al.* 1971; Hoffman & Stone, 1971; Fukuda & Saito, 1972; Hoffman *et al.* 1972; Hoffman, 1973; Cleland & Levick, 1974*a*; Fukuda & Stone, 1974; Wilson, Rowe & Stone, 1976). The fact that these

cells project to different central areas in the cat suggests that this diversity of cell types and information is maintained beyond the retina. The central projections of the different ganglion cells in the rabbit are not yet known.

Anatomy and physiology can be complementary approaches to the same problem. It is possible that the number of ganglion cells that can be differentiated physiologically is reflected in different morphologies of the cells. Boycott & Wässle (1974) were successful in correlating Golgi stained ganglion cell types in the cat retina with the W/X/Y cells, and Famiglietti & Kolb (1976) have suggested that on centre cells and off centre cells have dendritic arborizations that ramify in different strata of the inner plexiform layer. No similar study has been done in the rabbit. However, a recent Golgi study in ground squirrel (West, 1976) has identified at least fifteen morphologically different ganglion cells, based upon the stratification and branching pattern of dendrites. It would be useful to known whether the same anatomical diversity exists in the rabbit and to correlate the anatomy with the physiology.

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