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QUANTITATIVE ASPECTS OF SENSITIVITY AND SUMMATION IN THE CAT RETINA

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SUMMARY

1. Properties of the central response mechanism of on-centre ganglion cells in the cat retina were studied by recording, from optic tract fibres, responses evoked by stimuli modulated with time in a sinusoidal or square-wave fashion.

2. The shape of averaged square-wave responses resulting from the central mechanism alone was identified. This shape was identical from one cell to another. Such an identification permits the early recognition of peripheral antagonism.

3. Threshold sensitivity for a sinusoidal stimulus was determined for fifty cells along one horizontal and vertical axis, passing through the most sensitive portion of the receptive field. These sensitivity profiles were described in terms of a central segment of constant maximum sensitivity (uniform centre) and sloping outer segments of exponentially decreasing sensitivity (exponential annulus). The dimensions of the uniform centre (horizontal axis × vertical axis) varied from $0{\cdot}1° \times 0{\cdot}1°$ to $2{\cdot}5° \times 2{\cdot}2°$, the half width of the exponential annulus ranged from 0·1° to 0·63°.

4. Adapting spots of varying diameter were placed concentric with the receptive field and the (unmodulated) luminance, at each diameter, that reduced a small central (sinusoidal) stimulus to threshold, was determined. The resulting area–adaptation curve, (adapting luminance plotted against diameter) showed that within defined limits the state of adaptation is determined by the flux independent of its distribution.

5. Sinusoidal stimuli of varying diameter were placed concentric with the receptive field and the threshold luminance at each diameter was determined. Suprathreshold square-wave stimuli indicated that the

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central mechanism alone contributed to the response. These area-sensitivity curves did not show any decrease in sensitivity at larger diameters.

6. The shape of the area–sensitivity curve, and hence the extent of the summating area, was found to be independent of the state of adaptation.

7. For any one cell the shapes of the area–adaptation and area–sensitivity curves were shown to be identical, indicating that adapting flux and stimulus flux are independent of distribution over the same defined limits.

8. The sensitivity of combinations of small disconnected areas of the receptive field was found to be equal to the sum of their individual sensitivities.

INTRODUCTION

Kuffler (1952, 1953) originally described two concentric, mutually antagonistic areas that make up the receptive field of the majority of retinal ganglion cells in the cat. Even though central and surround responses are most easily elicited from their respective areas in the receptive field it is clear that there is also considerable spatial overlap. It is thus necessary to distinguish between two neurally interacting but functionally distinct *response mechanisms* (Wagner, MacNichol & Wolbarsht, 1963; Rodieck & Stone, 1965) termed the central and surround response mechanisms. The two mechanisms are conceived of as spatially overlapping, but each having its own receptor representation within the receptive field. Both mechanisms require investigation in terms of their distribution of receptor representation in the receptive field, summation properties, adaptation behaviour and their mutual interaction.

The experiments presented here deal exclusively with the central response mechanism and are intended to characterize its step response, to map its sensitivity over the receptive field and to describe its summation properties.

METHODS

Preparation and recording. In adult cats narcosis was initiated with diethyl ether and continued during preparatory surgery with repeated intravenous doses of thiamylal sodium, totalling 10–25 mg/kg. Light anaesthesia was thereafter maintained with urethane administered intravenously. Eye motions were suppressed with large doses of gallamine triethiodide (Cleland & Enroth-Cugell, 1966). The animal was respirated at 20–25 strokes/min and at a tidal volume determined by the weight of the cat (L. Kleinman and E. P. Radford, ventilation chart; Harvard Apparatus Co., U.S.A.). The body temperature, measured with a thermometer inserted under the scapula, was maintained at 38–39° C. No results here reported were obtained until at least 4 hr after the last dose of thiamylal.

Tungsten electrodes (Hubel, 1957) were stereotaxically placed in the optic tract. Action potentials from single fibres were amplified, displayed on an oscilloscope and monitored with a loudspeaker; the action potentials and stimulus signals were also recorded on magnetic tape. Contact lenses (range +2·0 to +4·5D), opaque except for a central trans-

parent zone of 4 mm diameter, were used to bring the stimulus to focus on the retina. A total of seventy-seven ganglion cells from twenty-six cats were included. Only on-centre cells were studied owing to difficulties arising when the central response mechanism is preferentially stimulated in off-centre cells.

Stimulation. Two fixed light sources (S_1 and S_2) positioned as shown in Fig. 1*A* were used. One source (S_1) was 125 cm from the cat's eye and consisted of seven small fluorescent tubes (Westinghouse F4T5/CW) mounted side by side behind opal glass. Neutral density filters and a wedge (Wratten No. 96) were placed in front of the opal glass in a filter holder (F_1). An indicator gave the density of the wedge to 0·01 log units. Next to the wedge was a black aluminium disk (A_v) with fifteen circular apertures whose diameter ranged from 3 to 60 mm,

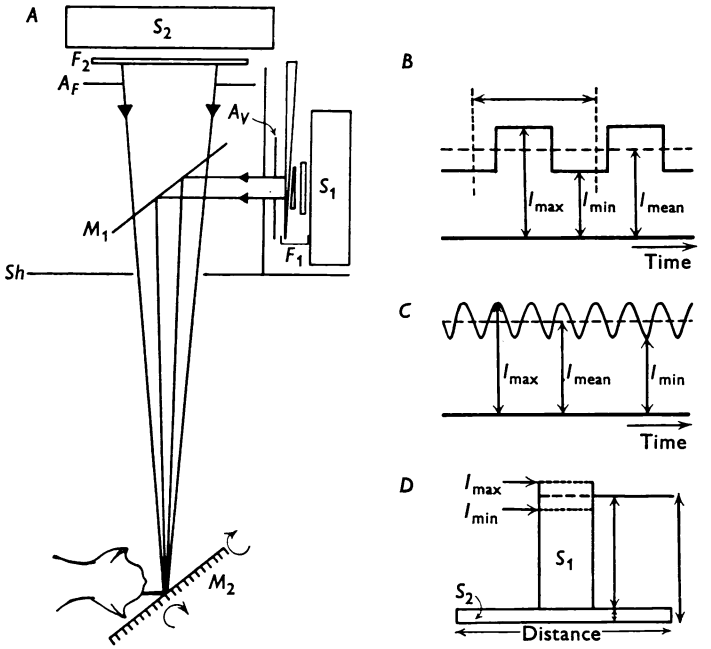

Fig. 1. *A*. Diagram showing the two light sources S_1 and S_2 and the optics of the system. The variable apertures of S_1 are contained in the disk A_v. The fixed aperture of S_2 is located in A_F. F_1 and F_2 are filter holders. S_1 is superimposed on S_2 with the half silvered mirror M_1. The two stimuli were moved in the visual field of the cat by adjusting the position of the mirror M_2. *B* and *C*. The two kinds of luminance modulation used in this study: slow square-wave stimulus (*B*) and sinusoidal (*C*). In both cases modulation depth is defined as $(I_{max}-I_{min})/(I_{max}+I_{min})$ expressed in per cent. In the figures of pulse density tracings that follow, 60 sequences as indicated by the horizontal arrow in *B* have been averaged. *D*. Schematic representation of the stimulus conditions during area–sensitivity experiments; sinusoidally modulated stimulus (S_1) superimposed on steady background (S_2).

the range of stimulus diameters in angle subtended at the cat's eye thus being 0·13°–2·50° (or approximately 0·03–0·63 mm on the retina). The tubes (luminance proportional to current) were supplied by a d.c. power source. Current was controlled by an electronic circuit driven by a function generator (Servomex LF 141) to give the desired time function of the luminance. Modulation depth is defined as: $(I_{max}-I_{min})/(I_{max}+I_{min})$ expressed in

per cent, where I is the stimulus luminance (Fig. 1 *B* and *C*). The frequency and the depth of modulation were set by the function generator while the mean level of the luminance was controlled by the neutral density filters and the wedge. The wave form of the stimulus was monitored by a photodiode set behind the fluorescent tubes so as to collect over as large an area as possible. The larger stimulator (S_2) was built on the same principle as the small one but with six fluorescent tubes (Westinghouse F15T12/CW). It had a single 17 cm (8·5°) aperture placed 114 cm from the cat's eye (A_f). Even though S_2 was generally not modulated, electronic control provided luminance stability. The luminance was attenuated as required with Wratten No. 96 neutral density filters (F_2). The maximum mean luminance of stimulus S_1 was 320 cd/m² and of S_2 500 cd/m² (measured with a Salford Instrument Photometer).

The two stimuli were superimposed by means of the half silvered mirror M_1 after which the light passed through a circular aperture (subtending 9° at the cat's eye) in a 100 × 100 cm metal sheet (*Sh*) which served as a uniform outer background. The inner background, i.e. the area immediately surrounding the stimulus spot, was provided by S_2.

The retinal image of the two superimposed stimuli could be moved to different positions with an adjustable first surface mirror M_2, placed immediately in front of the cat. This mirror could be rotated about both its horizontal and vertical axes to within 0·1° and was calibrated to give position within the visual field.

Data analysis. This was done during the experiment or at a later time using the data from the magnetic tape. With the aid of a smoothing network, a digital memory oscilloscope (Enhancetron 1024) and a X–Y plotter, the retinal ganglion cell spikes were converted into a plot of instantaneous pulse density versus time (Cleland & Enroth-Cugell, 1966).

RESULTS

Central type response

Our initial goal was to map the sensitivity distribution over the receptive field for the central mechanism alone, and so it was first necessary to characterize the pure central response, uninfluenced by surround effects. Experiments on fourteen on-centre cells showed; (*a*) that the response to a step function light stimulus of low luminance, restricted to the most sensitive portion of the receptive field, exhibited a pure central response, maintaining a constant form from time to time, from cell to cell and from animal to animal; (*b*) that an increase in light flux (either by luminance or area) by an order of magnitude or more resulted in a change in the transient response to a mixed form and (*c*) that these changes became far more pronounced, resulting in a classical surround response (spike frequency *peak* at 'off'), for a further increase in luminance. The characteristic pure central response thus proved easily distinguishable from a mixed response with even minimal surround antagonism.

Because of the importance of this finding to the present work, it is illustrated in more detail. Stimulus S_1, superimposed on a steady background of approximately 0 log td, was square wave modulated (Fig. 1 *B*) at a frequency of 0·4 c/s and a depth of 40 %. It was placed in the most sensitive portion of the receptive field, determined by auditing the response. With a small spot of fixed area the luminance was increased in one log

unit steps over a three log unit range. At each luminance sixty responses were averaged to yield a pulse density tracing. The results of such an experiment are shown in Fig. 2, where it can be seen that at the lowest mean luminance (Fig. 2, 1) the spike frequency shows a sharp increase at 'on' (the step increase in luminance) followed by a gradual decay to a small

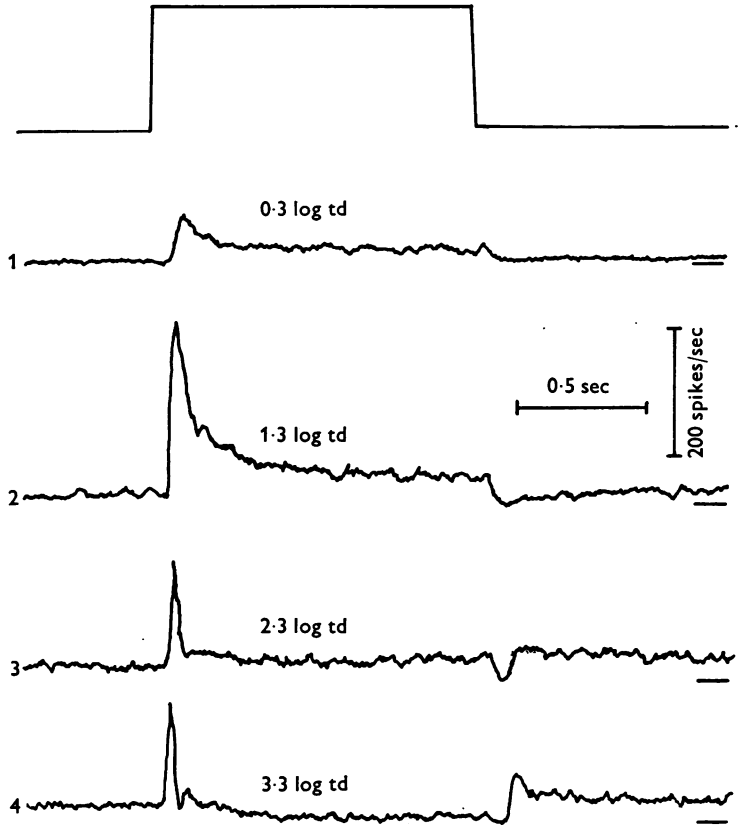

Fig. 2. Averaged responses to slow square-wave stimuli, frequency 0·4 c/s and depth 40 %. The stimulus was located in the most sensitive portion of the receptive field centre. The uppermost record gives the stimulus time course. Deflexion upwards indicates increasing luminance. The short horizontal line at the end of each record indicates zero pulse density. Background 0 log td. Stimulus size 0·13 deg and mean stimulus luminance as indicated above each record. Responses in 1 and 2 are purely central.

steady response; at 'off' (the step decrease in luminance) the spike frequency falls to zero followed by a gradual rise to a reduced steady level. Increasing the mean luminance by one log unit (Fig. 2, 2) only served to increase the height of the response but did not affect its form. A further increase in luminance (Fig. 2, 3) yielded a modified response; at 'on' the

peak was diminished, the decay accelerated and the steady response reduced. At 'off' the recovery from the initial fall was accelerated. Another order of increase in luminance (Fig. 2, 4) yielded a brief peak at 'on' while at 'off' a classical surround response was observed; after an initial fall the spike frequency rose rapidly to a *peak*, followed by a gradual decay.

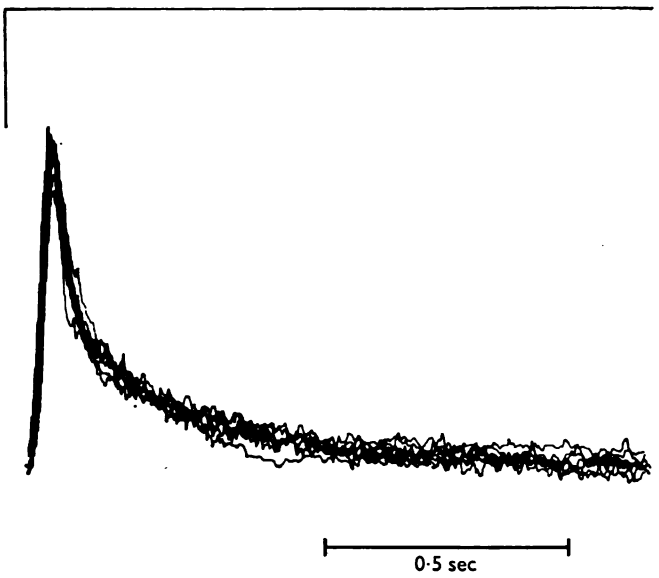

Fig. 3. Superposition of responses to slow square-wave stimuli (0·4 c/s, 40 % modulation) for seven on-centre cells. The stimulus was 0·13° and its mean luminance 1·3 log td in all cases. It was located in the most sensitive portion of the receptive field centre. The vertical scaling and position only have been adjusted. Deflexion upwards of the stimulus trace indicates increasing luminance.

Exactly the same sequence of events was observed when the mean luminance was held constant and the area of the stimulus was increased stepwise.

The important property of the low luminance, or pure central, responses was that they had exactly the same shape for all cells studied. For the same stimulus flux conditions the responses could be superimposed, using vertical scaling and translation, as shown in Fig. 3. For different flux conditions it was also necessary to translate the time axis for latency. Under no circumstances, however, was it ever possible to superimpose mixed responses as for pure central responses.

In the experiments to follow we determined thresholds by *listening* to the ganglion cell discharge while applying a stimulus modulated sinusoidally at 4 c/s. (Square-wave modulation would have served as well.) Although time conserving, this method is not very sensitive for the detec-

tion of minor surround effects. We therefore used *averaged* responses to slow (0·4 c/s) square-wave stimuli, of the same luminance as the threshold stimuli, as a sensitive test of whether the threshold responses were purely central.

Sensitivity profiles

Possessing now a convenient means of identifying a ganglion cell response generated by the central response mechanism alone, irrespective of the receptive field area from which it is elicited, spatial sensitivity profiles were determined across the receptive field for the *central* response mechanism. Since it has been shown that the receptive fields possess general symmetry (Kuffler, 1952, 1953; Rodieck & Stone, 1965; Enroth-Cugell & Robson, 1966), sensitivity measurements were limited to points along horizontal and vertical axes through the most sensitive portion of the field.

The stimulus S_1, diameter set at 0·13°, was superimposed upon a uniform background of approximately 0 log td. The spot luminance was sinusoidally modulated at a frequency of 4 c/s and constant depth. Thresholds were first determined at 0·5° intervals along the vertical axis through the most sensitive portion of the receptive field. The mean luminance, and hence the amplitude of the sinusoidal stimulus, was decreased by adjusting the position of the neutral density wedge until the experimenter just failed to hear a response, i.e. *a spike frequency fluctuation in synchrony with the stimulus.* The wedge density at threshold is a measure of the logarithm of the relative sensitivity, and was plotted against the vertical position of the stimulus in the visual field, as shown in Fig. 4. The resulting vertical sensitivity profile appeared quite symmetrical. The entire measurement procedure was then repeated at 0·5° intervals along a horizontal axis through the point of symmetry of the vertical sensitivity profile. The resulting horizontal sensitivity profile also appeared quite symmetrical so that a centre of symmetry for the receptive field could be defined. Horizontal and vertical sensitivity profiles were obtained in this manner for a total of 50 on-centre cells.

Such a pair of profiles, with a second set of measurements obtained 4 hr after the first, is shown in Fig. 4. They provide an excellent demonstration both of the stability of the preparation and of the ability of the investigator to maintain a constant threshold criterion. Figure 5*A–C* shows three more pairs of such profiles, one typical and the others the narrowest and widest obtained. For more than one half of the cells the experimental points clearly indicated an area of constant sensitivity across the central portion of the field while for the remainder the narrow profiles and coarse spacing of the points precluded such definition. All profiles exhibited an exponential decrease (linear on the log plot) in sensitivity on either side of the plateau, or peak. In the majority of cases the decrease was expo-

nential throughout, but in all cases exponential for at least one unit below the plateau, or peak. In the latter case the remainder of the fall was less rapid than exponential.

With the aid of averaged transient responses to slow square-wave stimuli (see p. 21) the threshold responses obtained from the plateaux and peaks of all the profiles were demonstrated to be purely central in nature as were the responses obtained from the points lying on the exponential portion of the profiles. On the other hand the lower, non-exponential

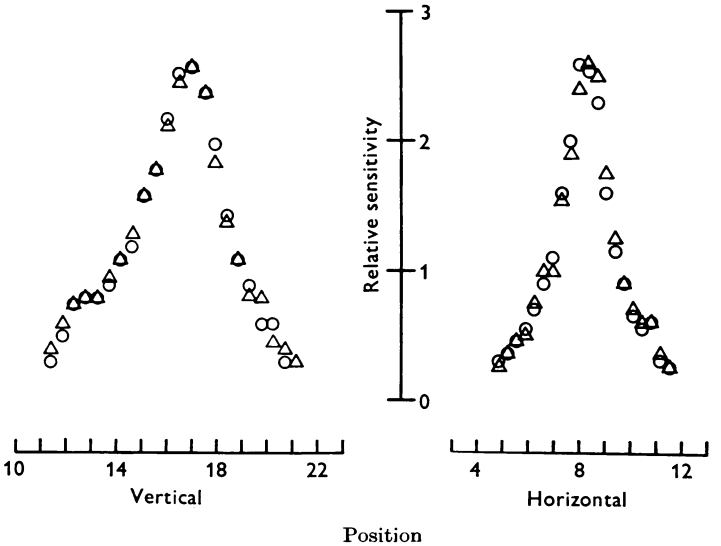

Fig. 4. Two sets of sensitivity profiles for the same cell to show example of the repeatability of threshold determination. Each point represents the sensitivity determined by ear with a 0·13° stimulus. The luminance was sinusoidally modulated at a frequency of 4 c/s and a depth of 60 %. Ordinates indicate relative sensitivity in terms of the lowest neutral density at which the experimenter just failed to hear a response (defined in text). The numbers along the abscissae give the stimulus position within the visual field in degrees. The origin of the co-ordinate system used lies on the line, normal to the Horsley–Clarke frontal plane, that passes through the centre of the artificial pupil. In the left-hand plots the numbers on the abscissa refer to positions along a vertical axis passing through the point of maximum response, in the right-hand plots to positions along a horizontal axis through the point of symmetry of the vertical sensitivity profile. Background approximately 0 log td. Zero on the relative sensitivity scale corresponds to 3·3 log td.

segments of the profiles were found to exhibit mixed responses with easily detectable surround influences. From these observations we concluded that the profile for the central mechanism consisted of a central plateau with exponentially falling sides.

In accordance with this conclusion, all profiles were fitted as illustrated

in Fig. 5. A horizontal line was drawn through the plateau points, and straight lines were drawn through the linearly aligned points on either side. The points of intersection of the horizontal with the two side lines defined the limits between the constant sensitivity and exponentially decreasing sensitivity portions of the receptive field for the central mechanism. The

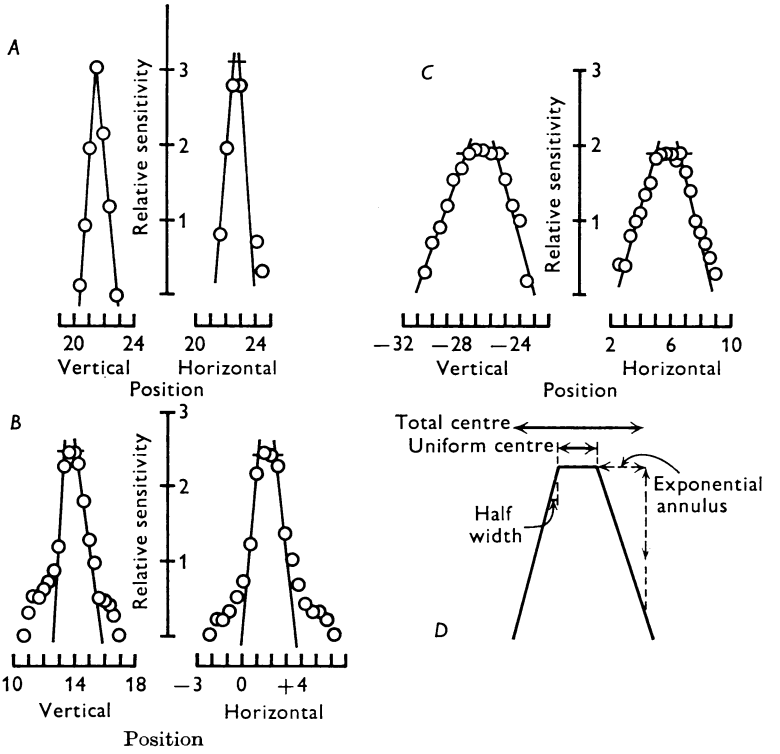

Fig. 5. *A–C.* Three sets of sensitivity profiles as in Fig. 4. *D.* Sketch explaining the graphical construction and the terms used for the quantitative description of the receptive field centres.

inner area of constant sensitivity will be referred to as the *uniform centre*, the annular zone as the *exponential annulus*. The latter can be described by its *half width*, defined as the angular width for the sensitivity to fall by 50 % (Fig. 5*D*) (0·3 log units). A *total centre* may arbitrarily be defined as the size of the receptive field when the sensitivity has fallen by 98 % (1·7 log units).

The dimensions (horizontal axis × vertical axis) of the uniform centre for the central type mechanism, in the fifty cells studied, ranged from 0·1° × 0·1° to 2·5° × 2·2°. In thirty-two of the fifty the ratio of the axes exceeded 1·2, with a maximum ratio of 6, suggesting that the majority of

uniform centres were elliptical. For two cells the sensitivity was determined at points on a 0·5° grid across the receptive field. Equisensitivity contours constructed on the basis of these measurements were roughly elliptical.

The half width of the exponential annulus ranged from 0·1° to 0·63° with a mean of 0·31°. The half width correlated positively with the size

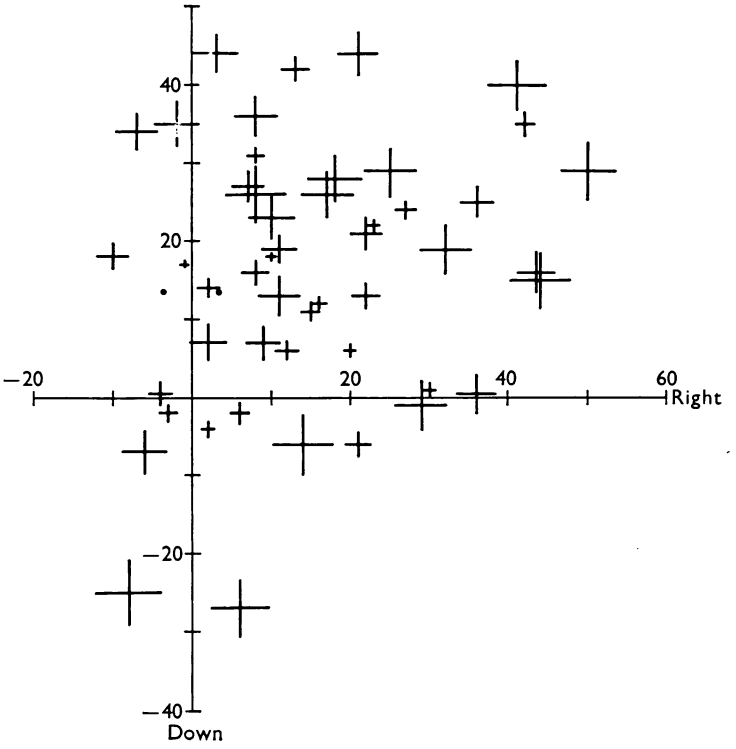

Fig. 6. Position in the visual field of all receptive fields for which sensitivity profiles were determined. The length of the horizontal and vertical bar of each cross is proportional to the horizontal and vertical axis respectively of the total centre. The origin of the co-ordinate system lies on the line, normal to the Horsley–Clarke frontal plane, that passes through the centre of the artificial pupil. The two filled circles above the x-axis show the average position of the presumed area centralis in cats paralysed with gallamine triethiodide (Vakkur, Bishop, Kozak & 1963).

of the corresponding uniform centre ($r = 0{\cdot}53$, $n = 50$, $P < 0{\cdot}01$). The total centres ranged from $1{\cdot}2° \times 1{\cdot}1°$ to $8{\cdot}1° \times 8{\cdot}4°$. The total centres of all cells and their positions in the visual field are shown by the horizontal and vertical bars in Fig. 6. These dimensions, of course, only apply to the central mechanism of the fields operating at threshold levels.

Artifacts are introduced into the results by the fact that the eyes do not

operate as perfect optical instruments. Light is scattered in an exponential fashion at the edge of any image; the normal measure for such an image spread is the distance on the retina required for the illumination to fall by one half. Westheimer (1962) measured the line-spread function in the cat's eye under conditions of best focus with the light entering along the visual axis. With a 6 mm diameter artificial pupil, he found the half width to measure 4–8 min of arc. We have used a 4 mm diameter artificial pupil and this should give slightly better results. However, we did not necessarily have best focus and the light usually entered off axis, in some cases by as much as 60°. We would therefore expect the half width of our image spread to be greater than 4–8 min of arc. For one third of the cells the measured half width of the exponential annulus was as small as 6–12 min of arc and thus may well be entirely due to image spread and focus error. Since image spread should be a function of distance from the optic axis, we have calculated the deviation from regression of the half width versus uniform centre width with distance from the optical axis but did not find a significant correlation ($r = 0{\cdot}24$, $n = 50$, $P < 0{\cdot}1$). However, the deviation tended to show a definite trend from cat to cat that was most likely related to focus error.

Adaptation

Visual adaptation is a change in sensitivity of the retina itself induced by exposure to light and Rushton (1965*a*) has described two forms: (1) *bleaching* adaptation which is slow, linked to the amount of unbleached visual pigment remaining in the retina and associated with a persistent after-image, (2) *field* adaptation which is a rapid change of sensitivity due to variations in the brightness of the surroundings, occurring over the whole range of vision, and *not* linked to the amount of visual pigment present.

During any determination of spatial variations in sensitivity within the receptive field, such as the sensitivity profiles already described or the summation experiments to be described, it is necessary to know whether bleaching adaptation is present and what conditions are required for maintaining constant field adaptation.

There are no data available for the cat regarding the relationship between bleached visual pigment and threshold. However, using Rushton's (1956, 1965*b*) data for man as a guide there is no reason to believe that the highest luminances used induced significant bleaching. To test this, an unmodulated stimulus of 2·5° diameter was projected onto the receptive field centres of three cells at 3·6 log td for a period of 4 min. The eye was then left in complete darkness for over 100 min for one cell and over 20 min for two cells, while thresholds were determined at 2 min intervals with a 0·13° diameter sinusoidally modulated stimulus located in the receptive

field centre. The maximum decrease in the last threshold over the first was 0·4 log units. Repetition of the experiment with an adapting spot of only 2·6 log td showed no measurable effect upon the threshold. Even the latter flux was far greater than those used for either the sensitivity profiles or the area–sensitivity curves. Further, these thresholds were determined against a completely dark background instead of 0 log td as used for all the sensitivity profiles and most of the area sensitivity curves. It is therefore reasonable to conclude that bleaching adaptation did not affect our sensitivity measurements.

The spatial summation experiments involve stimuli of varying area and luminance (see below) and hence field adaptation effects need investigation. The following experiments demonstrate that field adaptation remains constant so long as the light flux, within definable limits, remains constant.

The sinusoidal *stimulus* (from S_2) diameter was set constant at 0·13° and the mean luminance, modulated at 4 c/s and constant depth, was chosen so that it elicited a pure central response; its centre was aligned with the previously determined point of symmetry of the receptive field. A concentric unmodulated spot of *adapting light* of controllable luminance and diameter (from S_1) was then adjusted to reduce the response to the fixed stimulus to threshold. The area of the adapting spot was varied in fifteen steps from 0·13° to 2·50° by selecting the aperture in front of S_1, and for each such area the luminance (wedge position) was reduced until the previously audible response to the sinusoidal stimulus just disappeared. The filter density at threshold was then plotted against the logarithm of the diameter of the adapting spot, with results illustrated in Fig. 7*A*. A straight line with a slope of two provides a satisfactory fit to the initial portion of the curve and a horizontal line to the final portion, both lines being positioned to give zero mean error. The diameter, D_t, at which extensions of the two segments of the curve intersect, provides a complete description of the shape of the curve except for the fine detail of the transition from one slope to the other. Hence, the evaluation of D_t requires only that two points be determined on the curve; one on each of the sloping and horizontal portions. Five cells were studied in this manner and the only difference between them was the diameter at the point of transition.

A line with a slope of two on such a set of co-ordinates is a line of constant flux (area × luminance). Thus up to the diameter at which the curve diverges from the line with a slope of two, the state of field adaptation is determined by the light *flux* falling upon the receptive field and is independent of its spatial distribution. Moreover, a point anywhere on the horizontal portion of the curve indicates that light falling outside this diameter is without any effect upon the state of field adaptation.

Spatial summation

The dependence of threshold response, within defined limits, upon the total amount of retinal light flux, irrespective of its spatial distribution, is a well recognized phenomenon in psychophysical experiments. This reciprocal relation between the area and luminance of a stimulus that evokes a constant (threshold) response, known as Ricco's law, has also been investigated in a semi-quantitative manner at the retinal ganglion cell level in the cat (Barlow, Fitzhugh & Kuffler, 1957; Wiesel, 1960). The aim of the following experiments was to make a detailed study of Ricco's

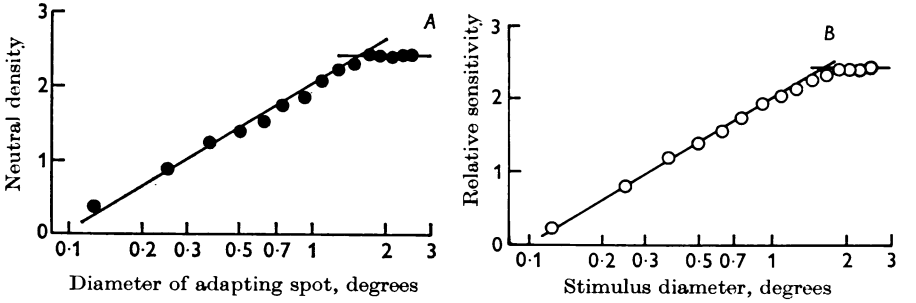

Fig. 7. *A*. Area adaptation curve. Stimulus S_2 was set at 0·13° and modulated at 4 c/s, and a depth of 60 %, about a mean luminance of 1·3 log td. Stimulus S_1 was used as an unmodulated adapting spot of varying diameter. At each diameter the luminance of S_1 was adjusted to bring the response to S_2 to threshold. *B*. Area sensitivity curve for same cell as above. S_1 was modulated at a depth of 60 % and 4 c/s. S_2 provided a fixed background of 0 log td. Both sets of results are the average of two determinations. Lines with a slope of two were drawn through the initial points and horizontal lines through the final points. The intersection in both cases occurs at the same diameter, i.e. $D_t = d_t$.

law and to observe the effect of changing the background luminance upon the limits of this law. In addition, the summating properties within the receptive field centre were studied with multiple small stimuli, spatially separated.

Area–sensitivity curves at threshold. The relation between stimulus area and threshold luminance, for responses evoked by the central response mechanism alone, was studied in a total of 26 on-centre cells with sinusoidally modulated spot stimuli. Stimulus S_1, made concentric with the receptive field centre, was modulated at 4 c/s and a constant depth, and superimposed upon an unmodulated background (S_2) (Fig. 1*D*). The diameter of the stimulus was varied in fifteen steps from 0·13° to 2·50°, and at each size, threshold was determined by reducing the mean luminance (adjusting the wedge position). The log relative sensitivity, in terms of

threshold density, was then plotted against the logarithm of the diameter to yield an area–sensitivity curve. For six of the twenty-six cells, area–sensitivity curves were obtained at more than one value of the background; for the remaining twenty cells the background was 0 log td. Results from this latter group will be treated first.

For all twenty cells the area–sensitivity curve exhibited an initial sloping segment and for twelve the curves extended to a final segment that was horizontal. A line with a slope of two (corresponding to Ricco's law) was drawn through the sloping segment of all curves (positioned to give zero mean error) and it provided an excellent fit for all but one cell. For this cell the sensitivity at larger diameters was slightly greater than would be expected, possibly due to eye movements and poor centring of the stimulus in the receptive field. Where appropriate, a horizontal line was drawn through the final segment of the curves. As in the previous section the intersection of the horizontal and sloping lines defines a diameter d_t which can be used to describe the shape of the curve, except for a small transitional range. The same area–sensitivity curves were obtained whether the area of the stimulus was changed in increasing or decreasing order. Furthermore, the fact that these responses were of a pure central type was established by examining averaged responses to slow square-wave stimuli of the same area and luminance as the sinusoidal threshold stimuli.

For six cells area–sensitivity curves were obtained at several backgrounds, one log unit apart, within the range $\bar{3}{\cdot}8$–$2{\cdot}8$ log td. This was carried out over five log units for one cell (Fig. 8), four log units for three cells and three log units for two cells. While for any one cell changes in the background had considerable effect upon threshold (i.e. position along the vertical axis), the value of d_t determined for each curve remained constant and independent of background.

The area–sensitivity curves and sensitivity profiles are basically just different measures of the spatial distribution of sensitivity within the receptive field. The initial sensitivity rise with a slope of two for the area–sensitivity curves indicates that the sensitivity per unit area of the receptive field, within the region obeying Ricco's law, is constant. This area (Ricco's) will correspond to the area of constant sensitivity determined from the sensitivity profiles, i.e. the uniform centre. Points on the horizontal portion of the area–sensitivity curve indicate that light falling beyond these areas has no effect upon the sensitivity, and must be outside the total centre. The transition range of the area–sensitivity curves will then correspond to the exponential annulus of the sensitivity profiles.

For a number of curves (eight), no horizontal segment was observed, probably due to a limitation on the maximum stimulus diameter (2·5°). For three of these eight cells horizontal and vertical sensitivity

profiles were also determined and the size of the uniform centre and slope of the exponential annulus was such that no horizontal segment would be expected below 2·5°.

The optical quality of the image is not as critical for determination of the area–sensitivity curves as for the horizontal and vertical sensitivity profiles (p. 26). In the area–sensitivity curves the initial segment with a slope of two is produced by the points at smaller diameters, and for all but

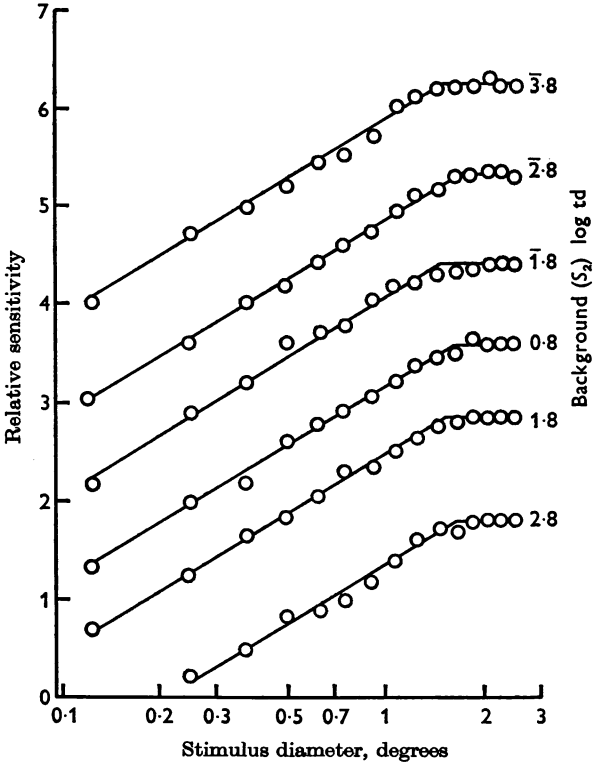

Fig. 8. Area–sensitivity curves for one cell at six steady backgrounds as indicated to the right of each curve. Zero on the relative sensitivity scale corresponds to a stimulus mean of 3·3 log td. Depth of modulation 60 %, stimulus frequency 4 c/s. Background diameter (S_2) is 8·5°.

the smallest field centres the image spread is contained well within the uniform centre and cannot therefore be a factor influencing threshold. On the other hand, at larger diameters, completely covering the centre and producing the final slope of zero, the flux contained in the image spread will not have any effect as it falls on areas that do not contribute to the central response. It is the transition from the initial to the final slope, as the image spreads out of the uniform centre, that will be the most susceptible

to poor image quality. As d_t is determined by the two segments of the curve unaffected by image quality, it will also be unaffected.

Area–sensitivity curves were determined for the same five cells used in the study of area adaptation effects (p. 28). The value of d_t, ranging from 0·8° to 2·0°, agreed closely with the value of D_t determined from the adaptation curves (e.g. Fig. 7). The average difference between the two was only 4% with a maximum of 8%, and can be considered negligible as it is within the repeatability of the determination of d_t for any one cell. Thus the mean luminance changes in such a way as to maintain a constant level of field adaptation and the only feature of the stimulus that need be considered is the sinusoidal variation. Our experiments can, therefore, be compared with those of other investigators (Barlow *et al.* 1957; Wiesel, 1960) who have used a constant background and determined threshold by intermittently flashing stimuli of increasing diameter upon this background.

In the same way that the use of a constant depth of modulation produces constant field adaptation in the determination of area–sensitivity curves, it will also produce constant field adaptation in the determination of the horizontal and vertical sensitivity profiles, as long as only the central response mechanism is stimulated.

Suprathreshold signal summation. Kuffler (1953) suggested that spatial sensitivity variations within cat retinal ganglion cell receptive fields are due to differences in the density of receptors functionally connected to the ganglion cell. On this hypothesis the density of receptors involved in the generation of a purely central response would be constant over the region defined as the uniform centre and would fall off exponentially beyond this (the exponential annulus). Thus we would expect the limits of Ricco's law to be independent of background luminance, as observed above, and we would also expect the summating properties to be the same at suprathreshold as for threshold levels.

In a series of experiments on eight cells, responses to square-wave stimuli of 0·4 c/s and a modulation depth of 40% were recorded and averaged. This was carried out at five spot diameters from 0·13° to 2·50° and with a luminance such that the flux remained constant. Several levels of stimulus flux were used on a 0 log td background. For all cells the responses could be superimposed for diameters within the limits obeying Ricco's law at threshold; beyond these limits the responses were decreased in magnitude. This suggests that the property of linear summation also occurs under suprathreshold conditions. Unfortunately, the experiments are not sufficiently critical for determining whether the limits are the same as those observed at threshold.

Multispot experiments. In the area–sensitivity experiments the successive increase in stimulus size was accomplished by adding annuli which were

concentric and continuous with a smaller circular stimulus. It can be argued that such experiments employ special conditions for the study of signal summation within the receptive field. Easter (1967) found in the goldfish that cells which exhibited Ricco's law, with circular concentric stimuli, did not sum sensitivities linearly when the light was distributed over disconnected areas in two spot experiments.

We did not find this to be so in the cat; the addition of sensitivities was linear within the receptive field centres of five cells on which we performed multispot experiments. A mask containing four circular 0·13° holes was placed in front of stimulus S_1 and these holes were spaced equally around

TABLE 1. Multispot experiment. Four spots of 0·13° diameter equally spaced around a circle of 1·3° diameter, concentric with the centre of the receptive field. 1, 2 and 3, 4 are opposite pairs of spots. On the left is shown the sensitivity for each spot individually. On the right the measured and calculated sensitivities for various combinations are compared

Single spots	Threshold density	Combination of spots	Measured threshold density	Calculated threshold density
No. 1	1·68			
No. 2	1·73	Nos. 1+2	2·03	2·01
No. 3	1·61	Nos. 3+4	2·04	1·98
No. 4	1·74	Nos. 1+2+3+4	2·31	2·29

the circumference of a 1·25° diameter circle which was concentric with the receptive field centre. The threshold sensitivity was determined for each spot individually, for opposite pairs of spots, and for all four spots together (sinusoidal modulation at 4 c/s). Table 1 presents the results for one cell and compares the sensitivities measured for the three combinations of spots with those calculated from the sums of the individual sensitivities. Each figure is the average of three determinations. The differences between calculated and measured sensitivities are negligible when one considers that the sensitivity can only be determined to 0·05 log units. For the other four cells each sensitivity was determined once and yet the maximum difference was only 0·1 log units. For one of the above cells, averaged responses to square-wave stimuli were also compared (modulation frequency 0·4 c/s and depth 40 %). The responses to each spot in an opposite pair were recorded separately at a mean luminance 0·6 log units above threshold, and for the two spots together 0·6 log units above the calculated threshold. All three responses were identical.

From these results and from our area–sensitivity experiments, it is evident that the summation of sensitivities is linear within the centre of the receptive field.

Prediction of area–sensitivity curves. Previous sections dealt with summating properties of the receptive field centre, as reflected in area–sensitivity curves and multispot experiments. If the observed sensitivity

of any one region within the centre is the sum of the sensitivities of its parts, then it should be possible to calculate an area–sensitivity curve based upon a sensitivity map of the centre of any cell. The experimental and the computed area–sensitivity curves can then be compared to provide one more argument on the summating properties of the centre.

We have used our horizontal and vertical sensitivity profiles to predict the relationship between area and sensitivity. The sensitivity $S(d)$, for any circular area of diameter d, can be obtained by integration;

$$S(d) = 2\pi \int_0^{\frac{1}{2}d} s(r) . r . dr,$$

where $s(r)$ is the average sensitivity per unit area of the horizontal and vertical sensitivity profiles at radius r. Plotting $S(d)$ versus d will give the predicted area–sensitivity curve. In Fig. 9 a curve calculated in this manner

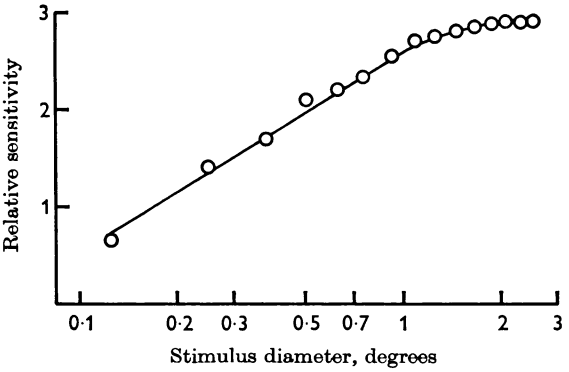

Fig. 9. The open circles are a plot of the diameter of stimulus S_1, modulated at 4 c/s and a depth of 60 %, against the relative sensitivity at that diameter. The solid line is the area–sensitivity curve calculated from the HV-profiles. Background 0 log td. Zero on the ordinate represents a mean luminance of 1·8 log td.

is shown together with the experimentally determined area–sensitivity curve of the same cell and the agreement between the two is seen to be excellent.

There are several experimental factors which may affect this agreement. First, if the horizontal and vertical axes of the sensitivity profiles are not the true major and minor axes of the central mechanism, then the area of the uniform centre, used in the calculations, will be smaller than the true area. Secondly, the determination of the sensitivity profiles, in particular the exponential annulus, is affected by the optical quality of the retinal image. Hence the predicted area–sensitivity curve and the value of d_t obtained from it will be susceptible to these errors.

As the diameter d_t provides a suitable description of the shape of the

area–sensitivity curve, a comparison of the value obtained from experimental and predicted area–sensitivity curves provides a convenient measure of the fit between these two curves. Such a comparison was made for seventeen cells. For two of these cells the agreement between the calculated and experimentally determined values of d_t was excellent (the one shown in Fig. 9 and another). For six more cells this agreement was reasonable, the difference between the two values of d_t being less than 20 %. For seven cells agreement between experimental and calculated values was poor. (For two cells both values were greater than 2·5°.) The poor outcome of these predictions may well be due to such experimental factors as suggested above. Two circumstances strengthen the suggestion that the sensitivity profiles failed to predict satisfactorily because of the large image spread, in some cases; the poorest agreement was in general seen in those cells that had the largest half width of the exponential annulus, and these were mostly found 24–36 hr after the start of the experiment. All but one of the area–sensitivity predictions showing reasonable agreement were from the first 12 hr. We routinely checked the corneal transparency at intervals, and obvious opacities could often be observed after 48 hr. However, it is quite conceivable that a corneal cloudiness sufficient to degrade the image quality passed unnoticed earlier in the experiment.

DISCUSSION

Granit's deduction (1955) that the changing balance between the on and off components of the retinal ganglion cell responses is 'one of the main exponents of interaction in the retina', preceded the demonstration of central and surround receptive field areas by Kuffler (1952, 1953), who also interpreted the changing discharge patterns in terms of retinal interaction. Since then centre–surround antagonism within concentrically organized receptive fields of cat retinal ganglion cells has been the subject of intense qualitative investigation. Our experiments on central type responses are but an extension of earlier work (Bishop & Rodieck, 1965), enabling us to establish criteria for a purely central response and for early detection of surround antagonism, prerequisites for a successful study of the central response mechanism independent of the surround response mechanism.

Our area–sensitivity curves differ from those of Barlow *et al.* (1957) and Wiesel (1960) in showing no tendency towards a sensitivity decrease at large diameters due to surround antagonism. This is a satisfying result since our aim was to stimulate the central response mechanism alone and to avoid surround antagonism. Some of our backgrounds (e.g. Fig. 8) were as high as those used by Barlow *et al.* and Wiesel and it is difficult to understand why their threshold responses were clearly mixed while ours were

not. However, there were appreciable differences in the time courses (frequency and wave shape) of the stimuli used and these could readily result in different threshold criteria.

Psychophysical experiments in man (e.g. Barlow, 1958) have shown that the retinal region over which complete summation takes place (Ricco's area) increases as the background luminance decreases. Also Barlow *et al.* (1957) concluded from ganglion cell experiments in the cat that a 'slight decrease in the size of the central, summating region of the receptive field' occurs as more light enters the eye. These changes would not appear to be sufficient to explain the psychophysical observations. Our experiments have shown that Ricco's area is a constant property of the receptive field centre of cat retinal ganglion cells, and the difference between our results and those of Barlow *et al.* is probably due to the fact that the latter observed surround antagonism for stimuli of larger diameter. The human and cat data become compatible if one assumes that as the background luminance in psychophysical experiments changes, new ganglion cells of different receptive field sizes are called upon for decision making—a mechanism suggested by Pirenne & Denton (1952) to explain human visual acuity changes. From our area–sensitivity curves and from multispot experiments we conclude that a linear addition of signals occurs within the initial processes of the retina contributing to the central mechanism. Rodieck & Stone (1965) reached similar conclusions based on superposition experiments with responses elicited from disconnected areas of cat receptive fields. Enroth-Cugell & Robson (1966) did not find linear summation over receptive fields of all cat retinal ganglion cells but these authors tested for linear summation of signals over the entire receptive field including the periphery.

Work of a quantitative nature has been done on retinal ganglion cell receptive fields in the cat (Barlow *et al.* 1957; Wiesel, 1960; Rodieck & Stone, 1965; Enroth-Cugell & Robson, 1966; Spinelli, 1966; Spinelli & Weingarten, 1966), but with regard to characteristics of the central mechanism it is often quite difficult to integrate the results of different workers; for instance, no two workers have used quite the same specifications for centre size. Moreover, sufficient information is rarely available for translation of one set of results into the terms of another investigator's results. We have attempted to provide a reasonably complete quantitative description of receptive field centres and to include such information as might be required for comparison between our results and those of others.

Enroth-Cugell & Robson (1966) assumed that the sensitivity of the centre and surround fell off as a Gaussian function of the distance from the centre of the receptive field. Their justification for this was that it led to a simple mathematical formulation and gave a satisfactory fit to their

experimental results. The difficulty with fitting a Gaussian curve is that there is only a single parameter. In contrast, the method described here permits the description of an elliptical area of constant sensitivity and an exponential annulus with a half width independent of the size of the uniform centre. That is, we are given three parameters which can be increased to four by a contour map of the sensitivity distribution, giving the orientation of the ellipse. While this provides a better description it is far more difficult to manipulate mathematically and the differences for the predicted results of Enroth-Cugell & Robson (1966) may be negligible. The greatest disparity is likely to occur for a receptive field with a large uniform centre and a small half width for the exponential annulus.

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