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THE CONTRAST SENSITIVITY OF RETINAL GANGLION CELLS OF THE CAT

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SUMMARY

1. Spatial summation within cat retinal receptive fields was studied by recording from optic-tract fibres the responses of ganglion cells to grating patterns whose luminance perpendicular to the bars varied sinusoidally about the mean level.

2. Summation over the receptive fields of some cells (X-cells) was found to be approximately linear, while for other cells (Y-cells) summation was very non-linear.

3. The mean discharge frequency of Y-cells (unlike that of X-cells) was greatly increased when grating patterns drifted across their receptive fields.

4. In twenty-one X-cells the relation between the contrast and spatial frequency of drifting sinusoidal gratings which evoked the same small response was measured. In every case it was found that the reciprocal of this relation, the contrast sensitivity function, could be satisfactorily described by the difference of two Gaussian functions.

5. This finding supports the hypothesis that the sensitivities of the antagonistic centre and surround summating regions of ganglion cell receptive fields fall off as Gaussian functions of the distance from the field centre.

6. The way in which the sensitivity of an X-cell for a contrast-edge pattern varied with the distance of the edge from the receptive field centre was determined and found to be consistent with the cell's measured contrast sensitivity function.

7. Reducing the retinal illumination produced changes in the contrast

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sensitivity function of an X-cell which suggested that the diameters of the summating regions of the receptive field increased while the surround region became relatively ineffective.

INTRODUCTION

Kuffler (1952) found that the receptive fields of light-adapted cat retinal ganglion cells are approximately circular and have functionally distinct central and peripheral regions; he showed that stimulation of these two regions produces opposite and antagonistic effects upon the activity of the ganglion cells. This concentric arrangement of receptive fields seems to be universal in both the cat and spider monkey (Wiesel, 1960; Hubel & Wiesel, 1960) and has also been found in the frog (Barlow, 1953) and rabbit (Barlow, Hill & Levick, 1964). It has been supposed that the receptive fields of the ganglion cells of the human retina have the same organization and it might therefore be expected that the characteristic behaviour of retinal ganglion cells would be closely correlated with the characteristics of human spatial vision, especially if measurements of the same kind were considered.

There have been many investigations of human spatial vision in both its acuity and contrast discrimination aspects (see reviews of Westheimer, 1965, and Boynton, 1962) but only one of the available methods of investigating the characteristics of spatial summation in the human visual system has been at all extensively applied to retinal ganglion cells. This method is the determination of the effect of size upon the increment threshold for a circular test patch. Barlow (1953) has used incremental threshold measurements of this kind to show that frog retinal ganglion cells respond to a linear combination of signals proportional to light intensity coming from all parts of their receptive fields. Barlow, Fitzhugh & Kuffler (1957) and Wiesel (1960) have also successfully employed the same method in studies of receptive fields in the cat retina and have briefly discussed the relation of their results to visual acuity and simultaneous contrast phenomena.

In studies on retinal ganglion cells the activity of the inhibitory surrounds of retinal receptive fields is clearly demonstrated by the existence of an optimal diameter for the test patch. But psychophysical determinations of the threshold contrast for disks of various diameters (e.g.Barlow, 1958) show that there is no optimal diameter for a test patch. To explain this difference it has been postulated that the inhibitory effects within the receptive fields of individual ganglion cells in the human retina are obscured by the mode of operation of the central mechanism responsible for detecting changes in the discharge in the optic nerve (Glezer, 1965). However, it is obviously desirable to investigate spatial summation in animal retinas

with techniques which, when applied to the human visual system, do not obscure any inhibitory retinal interactions.

A particularly promising technique was introduced by Schade (1956) who measured the visibility of grating patterns having a luminance which varied sinusoidally with distance perpendicular to the direction of the bars. He found that the threshold level of contrast for detecting such patterns was a function of the spatial frequency of the grating and showed a clear minimum at a spatial frequency which varied with the mean luminance. He interpreted the fall in sensitivity at higher spatial frequencies as the joint effect of optical blurring and retinal summation and the fall in sensitivity at lower spatial frequencies as the effect of retinal inhibition.

We now report measurements of the responses of cat retinal ganglion cells to sinusoidal grating patterns of the kind employed by Schade. In particular we consider the relation between the contrast and spatial frequency of grating patterns which evoke the same (small) response from a ganglion cell; this relation provides a description of the spatial summation within the receptive field of the cell which can be directly compared with the psychophysical results of Schade (1956) and others. We also consider the usefulness of the 'contrast sensitivity function' of a ganglion cell (the reciprocal of the relation described above) in predicting the sensitivity of the cell to other patterns. This amounts to a consideration of the linearity of the retinal summation process, for it is only within the limits of linearity that the techniques of Fourier analysis and synthesis (the techniques required for using the contrast sensitivity function) can be applied.

METHODS

Preparation and recording. Experiments were conducted on adult cats anaesthetized with an initial 40–80 mg/kg intraperitoneal injection of thiopentone sodium. Additional thiopentone was given intravenously in single doses at an average rate of about 1·5 mg/kg.hr when the experiments lasted more than 10–12 hr. Preliminary experiments (without muscle relaxants) showed that this procedure maintained anaesthesia satisfactorily. To suppress eye movements succinylcholine chloride was administered by continuous intravenous infusion at rates of 7·5–25 mg/kg.hr in a glucose and dextran solution. For those experiments in which the effect of varying the position of a grating or an edge within the receptive field was studied (see Figs. 1, 3, 12–14) immobilization of the eyes was particularly critical and dose rates of approximately 20 mg/kg.hr were always required. Body temperature was maintained at 38° C.

The cat's head was fixed in a stereotaxic instrument and a rectangular piece of bone together with the underlaying dura was removed from the top of the skull. This opening lay directly above the optic chiasm and that portion of the optic tract above which there is no geniculate body (Jasper & Ajmone-Marsan, 1954). Tungsten electrodes with a tip diameter of approximately 0·5 μ (Hubel, 1957) were used. The electrodes were held in a manipulator with hydraulically controlled vertical motion, modified after Hubel (1959). A vertical wall of dental impression compound around the hole in the skull together with the base plate

of the hydraulic electrode-positioner (pressed against the compound while this was still soft) formed a closed chamber above the exposed cortex. This chamber was filled with mineral oil through which the electrode entered the brain.

In preliminary experiments it was confirmed histologically that when the Horsley–Clarke co-ordinates (Jasper & Ajmone-Marsan, 1954) indicated that the electrode tip was in the optic tract it actually had been located there. No visual responses were obtained above Horsley–Clarke $H-1{\cdot}5$ to $H-2{\cdot}0$ in those animals in which the location of the electrode tip was not histologically determined. Further, in each experiment the positions of all the penetrations producing any visual responses were combined into a map which always corresponded to the known course of the optic tract. We are confident that the recordings obtained in all our experiments originated in optic-tract fibres even when there was no direct histological confirmation of the electrode position.

Both eyes were atropinized and phenylephrine hydrochloride was applied to retract the nictitating membranes. Contact lenses of $+5{\cdot}5$ D were applied to each eye with a standard contact-lens fluid. The cat faced the stimulus screen at a distance of 23 cm. For most animals the $+5{\cdot}5$ D contact lenses provided close to the best possible focus of the pattern on the retina. If necessary, additional spectacle lenses were placed 1 cm in front of the eye. A 3·5 mm diameter pupil was usually placed just in front of the contact lens whenever the receptive field of the unit being studied was not more than about 30 deg from the optic axis of the eye. When the receptive field was more eccentric than this it was not possible to locate an artificial pupil in such a way as to be sure that there was no vignetting of the retinal image and in these cases no artificial pupil was used. When it was desired to decrease the retinal illumination neutral-density filters were placed immediately in front of the cat's eye.

The action potentials from single optic-tract fibres were amplified in a conventional manner, monitored over a loudspeaker and on an oscilloscope and recorded on magnetic tape together with the necessary stimulus signals. During the experiment the mean frequency of the nerve discharge could be determined by counting the pulses with an electronic counter for periods of 10 sec.

Recordings were obtained from a total of 128 optic-tract fibres in thirteen cats and the behaviour of ninety-seven ganglion cells in response to grating patterns was studied. No exact method of determining the location of a receptive field was employed but the angles between the line connecting the eye with the centre of the receptive field and the horizontal and vertical planes were estimated to within 5 deg. These angles were corrected for the direction of the optic axes in cats paralysed with succinylcholine (Vakkur, Bishop & Kozak, 1963) to provide an estimate of the angular position of the projection of the receptive field relative to the centre of the area centralis.

Stimulus. The stimulus pattern was provided by a cathode-ray tube display (Campbell & Green, 1965). This gave great flexibility and ease of control and made it possible to change the contrast of a pattern without affecting its mean luminance level. The cathode-ray tube used was of the kind provided in the Tektronix 502 A oscilloscope but had a P-31 (blue-green) phosphor. The tube was physically removed from an oscilloscope but it remained electrically connected by a flexible lead. The tube was contained in a magnetic screening shield and mounted on a large adjustable stand so that its fluorescent screen could readily be placed at a distance of 23 cm from the anterior nodal point of the cat's eye. It was positioned so that the centre of the receptive field of the retinal unit from which recordings were being made projected to the middle of the screen, which was perpendicular to the line joining the cat's eye and the centre of the projection of the receptive field. The screen of the cathode ray tube was masked so that only a square of 8·5 cm side was exposed; the illuminated area subtended about $21° \times 21°$ at the cat's eye.

The screen of the cathode-ray tube was apparently evenly illuminated to a level of 16 cd/m^2 by deflecting the beam vertically at 150 kc/s with a triangular wave while the time base provided a sawtooth wave form at 225 c/s to scan it horizontally. The frequency of the

time base was much higher than the critical fusion frequency for retinal units in the cat (Dodt & Enroth, 1954; Grüsser & Reidemeister, 1959) and the number of vertical lines in the raster (about 1500) was much greater than the number that could be resolved on the screen of the cathode-ray tube. It thus seems reasonable to suppose that the screen was effectively steadily and uniformly illuminated for the cat as well as the experimenter.

To produce grating patterns upon the otherwise uniformly illuminated screen a suitable periodic modulating voltage was applied to the grid of the cathode-ray tube. The time base generator was normally triggered by a signal derived from the modulating voltage generator so that the time base and modulating voltage were synchronized to produce a steady pattern on the screen. The phase relation between the trigger signal and the modulating voltage was continuously variable, allowing the position of the pattern on the screen to be continuously varied. The variable phase relation between trigger signal and modulating voltage was achieved by supplying the field windings of a synchro resolver (e.g. Ahrendt, 1954) with sine and cosine waves from the modulating voltage generator and using the output signal from the rotor winding to trigger the time base. The relative phase of the output from the rotor was directly determined by the angle between the rotor and stator of the resolver and hence the displacement of the pattern on the screen could be read directly as a relative phase angle from a scale on the shaft of the resolver.

For some experiments the resolver was driven at a constant speed by a synchronous motor. This caused the grating pattern to drift at constant velocity across the screen. With this arrangement the velocity of the movement of the grating was such that at any spatial frequency the temporal fluctuation of luminance at any point on the screen was equal to the rotational frequency of the resolver (drift frequency).

The contrast pattern on the oscilloscope screen was presented in two forms—stationary or moving. When stationary, the pattern was not continuously present but was alternately introduced and withdrawn by switching on and off the modulating voltage. Thus the screen was alternately patterned and uniformly illuminated. In describing the results of experiments with stationary contrast patterns the expression 'phase angle of the pattern' will be used in the specific sense of indicating the position of the cosine grating pattern relative to the centre of the receptive field of the cell (see right-hand sketches in Fig. 1).

The amplitude of the modulating voltage could be adjusted to vary the contrast of the pattern. Contrast is defined as $(L_{max.} - L_{min.})/(L_{max.} + L_{min.})$, where L is the stimulus luminance. The contrast of the grating was standardized with a calibrated neutral-density filter (Campbell & Green, 1965). It was found that there was a proportional relation between the modulating voltage and the contrast of the pattern for contrasts of up to 0·45, the maximum value used in these experiments. The modulating voltage was arranged to have a mean of zero and so the mean luminance of the screen was not changed when the modulating voltage was switched on.

Data analysis. The change in the discharge in an individual optic nerve fibre produced by the presentation of a visual stimulus is not usually well defined, particularly when the stimulus is small. It is therefore useful, when investigating the activity of a single ganglion cell, to consider some kind of average response to repeated presentations of a stimulus. The form of average that has previously been used (e.g. Kozak, Rodieck & Bishop, 1965) is the averaged response histogram. This function is the average number of impulses that occur in each unit time interval after the stimulus presentation. In the limit (as the unit time interval is made vanishingly short) this becomes an estimate of the average 'pulse density' of the response. In a practical situation it is necessary to compromise between decreasing the unit time interval to achieve adequate time resolution and increasing the time interval to provide a usefully smooth function. As an alternative to increasing the unit time interval it is possible to use a very short time interval and a separate linear low-pass filter to provide the smoothing. In this way no extra loss of information is introduced by the smoothing. The filter can, of course, precede the averaging mechanism and this is the arrangement that we have adopted.

The nerve impulses were used to trigger a pulse generator giving current pulses of 0·5 msec duration. The current pulses were fed into a capacitor which discharged through a fixed resistor, the time constant of the combination generally used being 20 msec. The voltage across the capacitor was applied to an 'averaging' computer which formed the sum of a number of responses (generally eighty) with a time resolution of 1 or 2 msec. This sum was scaled to give a smooth estimate of the average pulse density of the response.

RESULTS

Stationary patterns

General. In initial experiments the response of ganglion cells to the presentation of stationary patterns was examined. It was found, as expected, that the magnitude of the response was dependent upon the position of the pattern with respect to the receptive field centre, i.e. upon the phase angle of the grating (as defined on p. 521). However, it was evident that the way in which the response changed as the phase angle of the pattern was varied was not the same for all ganglion cells but rather that there were two types of cell exhibiting distinctly different behaviour. Cells of the two types will be referred to subsequently as X-cells and Y-cells; both on-centre and off-centre varieties of both cell types were found (X-cells: nineteen on-centre and six off-centre; Y-cells: forty-six on-centre and fifty-seven off-centre).

The difference in the behaviour of X- and Y-cells can be seen by comparing Figs. 1*A* and 1*B* which show, respectively, typical responses of off-centre varieties of the two types of cell. As a general description of the difference of form of the two sets of responses it may be said that the responses of the Y-cell are more complex than those of the X-cell; in particular the responses of the X-cell to the introduction and withdrawal of the pattern are more nearly the inverse of each other than is the case for the Y-cell. However, the most characteristic difference in behaviour is to be seen by comparing the responses for the grating phase angles of 90 deg and 270 deg (see Fig. 1). These are the positions in which the pattern lies with odd symmetry about a diameter of the receptive field and in which the changes in luminance over one half of the receptive field are the exact inverse of the changes over the other half. For these two positions X-cells do not respond at all to introduction and withdrawal of the pattern while Y-cells respond with large increases in pulse density both when the pattern is introduced and when it is withdrawn. Moreover, the particular phase angles at which grating patterns do not stimulate X-cells are not dependent upon the contrast of the pattern. This is exemplified by the finding that whenever 'null positions' for a grating can be shown to exist they always occur 180 deg apart; that is, the phase angle of a null position does not depend upon the sign of the contrast.

Furthermore, neither the existence nor the phase angle of a null position depends upon the mean luminance of the pattern.

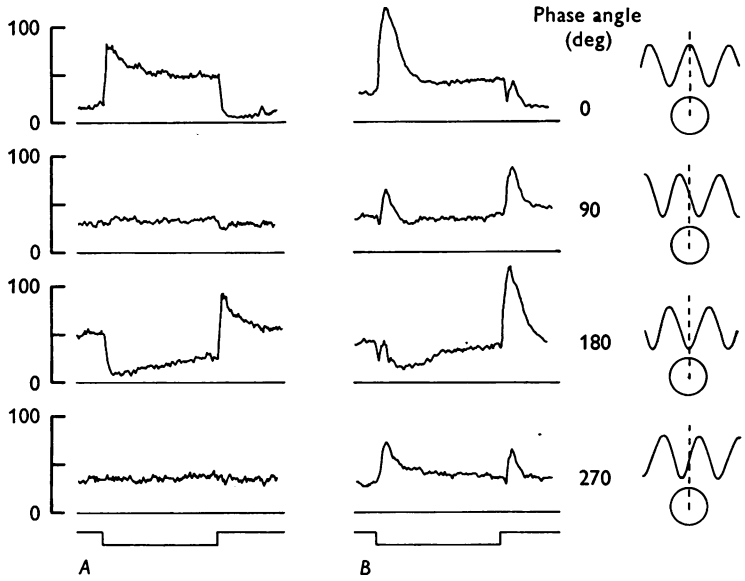

Fig. 1. Responses of an off-centre X-cell (*A*) and an off-centre Y-cell (*B*) to the introduction and withdrawal of a stationary sinusoidal grating pattern. The contrast (0·32) was turned on and off at 0·45 c/s. Downward deflexion of the lowest trace in both *A* and *B* indicates withdrawal of the pattern (contrast turned off), upward deflexion indicates introduction of the pattern (contrast turned on). The upper line in each pair is the pulse density of the ganglion cell discharge (scale at left: pulses/sec); the length of the zero line represents a duration of 2 sec. The 'phase angle of the pattern', i.e. the angular position (in degrees) of the (cosine) grating relative to the mid point of the receptive field centre, is given at the right of the figure and is illustrated by the sketches. *A*: X-cell (no. 84); spatial frequency 0·13 c/deg. *B*: Y-cell (no. 13); spatial frequency 0·16 c/deg.

X-cells. From these findings relating to the existence of null positions for grating patterns it is possible to draw certain conclusions about the characteristics and interaction of the photoreceptor signals which sum to affect the discharge of X-cells. At this point it may be helpful to recall in a simple diagrammatic fashion (Fig. 2) the picture that we have in mind when discussing the implications of these null position findings. We assume that each retinal ganglion cell is influenced by signals coming from elementary areas of its receptive field (photoreceptors) and that each receptive field is organized into an approximately circular central region with a concentric surround (Kuffler, 1953; Rodieck & Stone, 1965*b*). We assume that signals from all the elementary areas that together constitute the 'centre summating region' are summed to provide one signal (*C* in Fig. 2) while signals

from all the elementary areas that constitute the 'surround summating region' are separately summed to provide another signal (S of Fig. 2). The summated signals C and S have antagonistic effects upon the ganglion cell. Although retaining the term 'surround' we visualize the surround and centre summating regions as being co-extensive in the central part of a receptive field (cf. Rodieck & Stone, 1965*b*). This notion is illustrated by the way in which the weighting functions of the centre and surround summating regions have been drawn in Fig. 2.

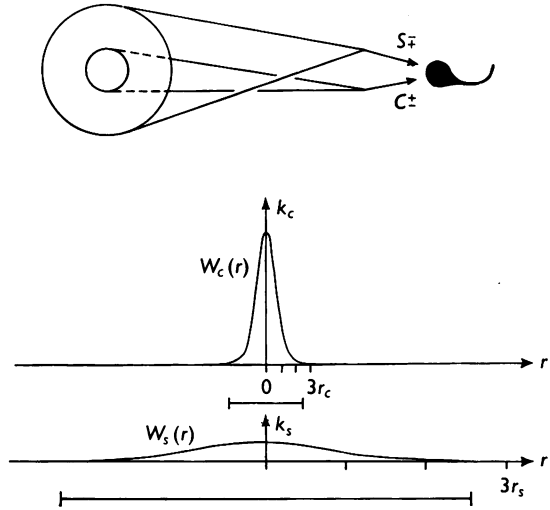

Fig. 2. Diagrammatic representation of signal summation over a retinal ganglion cell receptive field. The upper diagram illustrates the assumption that signals from elementary areas constituting the centre summating region and signals from elementary areas constituting the surround summating region are separately summed and that the resulting signals C and S have antagonistic effects upon the ganglion cell. For an on-centre cell the two signals would be described by $+C$ and $-S$, for an off-centre cell by $-C$ and $+S$. In the lower half of the figure are shown the Gaussian weighting functions assumed to describe the sensitivities of the centre and surround summating regions respectively; $W_c(r) = k_c \exp[-(r/r_c)^2]$. $W_s(r) = k_s \exp[-(r/r_s)^2]$ (see pp. 534–535). Note that the weighting functions for both centre and surround summating regions have maxima in the middle of the receptive field. The bars drawn below the centre and surround weighting functions are $5r_c$ and $5r_s$ long respectively. These bars indicate the assumed 'anatomical' diameters of the regions.

From the very existence of null positions it can be argued that the time course of changes in the signals from photoreceptors whose illumination is suddenly increased must be substantially the inverse of that of changes in signals from photoreceptors whose illumination is suddenly decreased for the sum of such signals can evidently remain constant. This implies either that the signals from photoreceptors are linearly related to their illumination

or that they are non-linearly related in a way which is symmetrical about the mean luminance. The latter alternative can be ruled out by the observation that the null positions for grating patterns are not changed when the mean luminance is changed. It can therefore be concluded that X-cells respond to the sum of a number of signals from different parts of their receptive field, each proportional to the local retinal illumination. This is not to say that the response of an X-cell is linearly related to the contrast or luminance of the stimulus (it clearly is not so related) but only that the initial processes of photoreception, signal transmission and signal summation are linear. A proviso is in fact required if it is assumed, as we have, that the excitatory and inhibitory signals (C and S of Fig. 2) that interact to affect the ganglion cell result from two separate processes of spatial summation; in this case, although we can certainly conclude that the separate processes of summation are linear we have not *demonstrated* that the interaction of the summed excitatory and inhibitory signals is also linear (subtractive).

Y-cells. Y-cells clearly respond to both the introduction and the withdrawal of grating patterns whatever the position of the pattern (Fig. 1*B*). There is, however, considerable variation in the form of the response that is evoked by such a stimulus; indeed, for each cell the form of the response is usually dependent upon both the contrast of the grating as well as its spatial frequency. Many of the cells respond with a large transient increase in pulse density to both the introduction and withdrawal of the pattern (Fig. 3). These transient responses become more nearly the same at every position of the pattern as the spatial frequency is raised (cf. Figs. 3*A* and *B*) although this is accompanied by a general reduction in the magnitude of the response.

The behaviour of the Y-cells is evidently very non-linear and indeed it seems likely that these cells respond to any change in the light distribution over their receptive fields. If linear summation of signals from the photoreceptors which influence these cells occurs at all it must do so only over small regions of the whole receptive field.

Moving patterns

The magnitude of the response of a ganglion cell to the presentation and withdrawal of a stationary grating pattern was found to be dependent not only upon the position of the pattern but also upon its contrast and spatial frequency. A few determinations were made of the effect of changing the spatial frequency and contrast of the gratings upon responses to the presentation of stationary patterns (e.g. Fig. 3), but it was found difficult to achieve the long-term positional stability of both the stimulus display and the cat's eye which was necessary for studying the higher spatial frequencies.

A simplified technique was therefore adopted; this was based upon the use of sinusoidal grating patterns drifting steadily in a direction perpendicular to their bars.

Under these conditions of stimulation the luminance at each point of the receptive field of a ganglion cell is modulated sinusoidally in time about some mean level, the depth of modulation of the luminance being the same as the contrast of the pattern. Since the responses of ganglion cells are evidently the result of time-dependent processes in the retina, it is

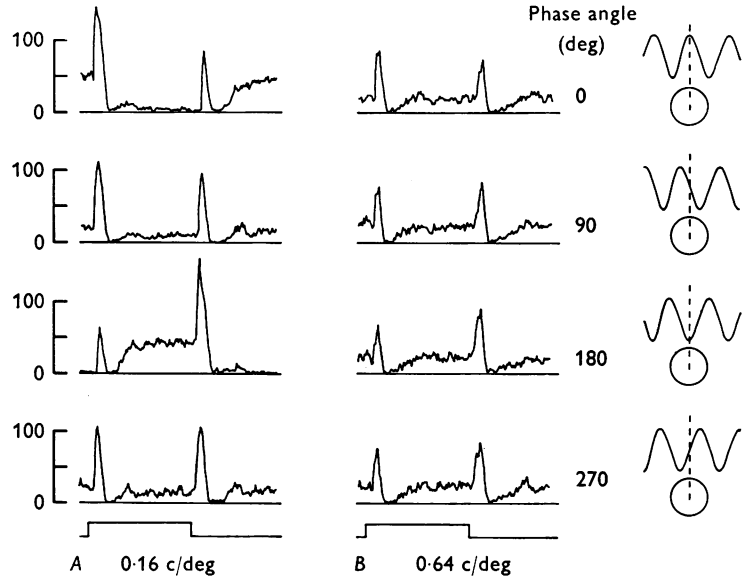

Fig. 3. Responses of an on-centre Y-cell (no. 20) to the introduction and withdrawal of a stationary grating pattern of low spatial frequency (*A*) and higher frequency (*B*). The contrast (0·32) was turned on and off at a temporal frequency of 0·45 c/s. The upper line in each pair is the pulse density of the ganglion cell discharge (scale at left: pulses/sec); the length of the zero line represents a duration of 2 sec. The lowest traces indicate the introduction (upward deflexion) and withdrawal (downward deflexion) of the pattern. The phase angle of the pattern is given to the right of the records.

essential that the temporal characteristics of stimuli whose effects are to be compared should be the same. For grating patterns of different spatial frequency drifting at constant velocity this is achieved if the velocity is inversely proportional to the spatial frequency; in this way the temporal (drift) frequency of luminance changes is kept constant.

By using a moving pattern as a stimulus, the magnitude of the response of a cell to a grating having certain contrast and spatial frequency is defined by just one measurement instead of by a series of measurements for different positions of the pattern.

In the experiments reported here the velocity was generally such as to produce a temporal fluctuation of 1 c/s. At times it was adjusted to produce a temporal fluctuation of 4 c/s. These frequencies were chosen because they appeared to be in the approximate frequency region in which the maximum amplitude of response was obtained. The amplitude of the responses always fell off markedly at temporal frequencies above 15 c/s and appreciably at frequencies below 1 c/s.

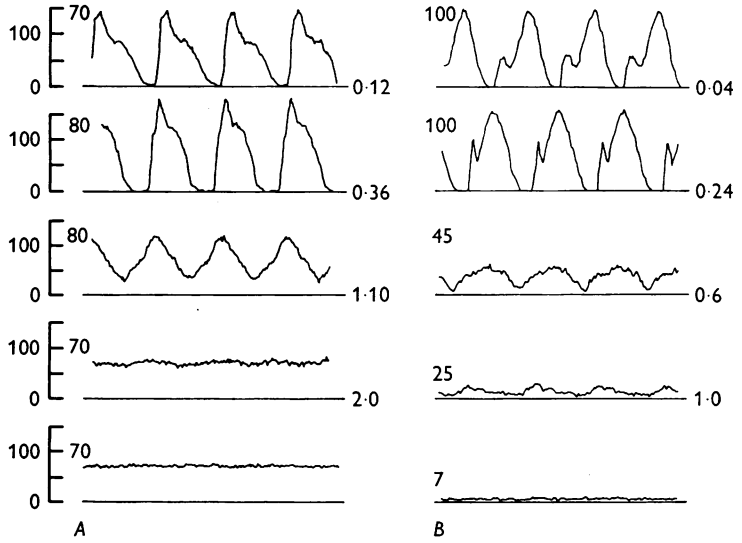

Fig. 4. Responses from (*A*) an on-centre X-cell (no. 128) and (*B*), an off-centre Y-cell (no. 103) to sinusoidal grating patterns of different spatial frequencies but the same contrast (0·4) drifting across their receptive fields. For each spatial frequency the velocity at which the grating drifted was such as to modulate the luminance of any point at 4 c/s (the 'drift frequency'). The upper line of each pair is the pulse density (scale at left: pulses/sec); the length of the zero line represents 1 sec. The spatial frequency (c/deg) is shown at the right of each zero line. The lowest records in (*A*) and (*B*) show responses to a uniformly illuminated field. The mean pulse density of the discharge (pulses/sec) is given to the left of each pulse density trace.

Figure 4 shows the responses of one X- and one Y-cell to the passage across their receptive fields of gratings of various spatial frequencies but of fixed contrast. The pulse density is modulated with an obvious periodicity at 4 c/s, the drift frequency in this particular experiment. The amplitude of the modulation is clearly greatly reduced at high spatial frequencies and somewhat reduced at spatial frequencies below an intermediate optimum value.

The wave form of the Y-cell (Fig. 4*B*) response is typically more distorted than that of the X-cell (Fig. 4*A*), in much the same way as with the

stationary patterns. However, the most striking difference between X- and Y-cell behaviour lies in the effect of the drifting pattern upon the mean pulse density. X-cells respond to movement of the pattern with a periodic modulation of the pulse density of their discharge without producing any change in its mean value. Y-cells on the other hand respond with a large increase in the mean pulse density upon which background discharge the periodic modulation is superimposed. Indeed some Y-cells do not discharge at all when steadily illuminated, only doing so when there is some temporal variation in the retinal illumination. It should be noted that although the X-cell of Fig. 4 has an on-centre and the Y-cell an off-centre the differences in behaviour of X- and Y-cells are not simply a question of different centre types. This is exemplified by the differences in the responses to stationary patterns shown in Fig. 1 where the X- and the Y-cell have the same type of centre. It is, however, true that the majority of the X-cells had an on-centre (see p. 522).

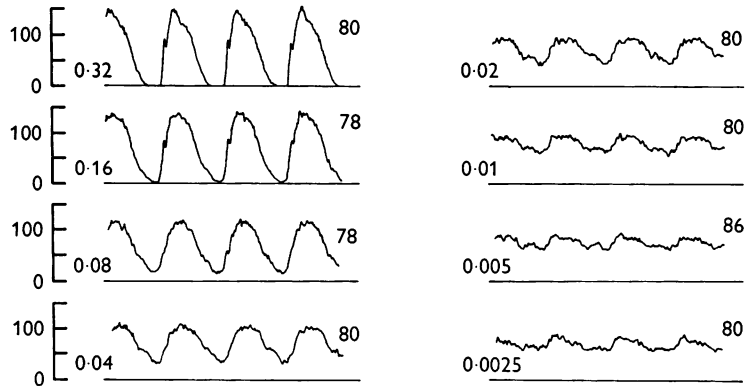

Fig. 5. Responses from an on-centre X-cell (no. 128) to drifting sinusoidal grating patterns of constant spatial frequency (0·36 c/deg) but different contrasts (contrast given at the left of each record). The drift frequency was 4 c/s. The upper line of each pair is the pulse density (scale at left: pulses/sec); the length of the zero line represents 1 sec. The number to the right of each record is the mean pulse density (pulses/sec) of the discharge of the cell. Note that in no case does the peak-to-peak response amplitude double when the contrast is doubled and that the wave form of the pulse density modulation does not appear to become more sinusoidal as the contrast is reduced to very low values. The experimenter could hear the modulation of the frequency of the discharge when the contrast was greater than 0·015.

For drifting gratings of any given spatial frequency the magnitude of the response of a ganglion cell increases with increasing contrast of the pattern. Figure 5 illustrates the effect of changing the contrast of a drifting grating of fixed spatial frequency upon the discharge of an on-centre X-cell. An obviously non-linear distortion of the wave form of the modulation

of the pulse density is evident for the higher contrast levels when the pulse density becomes zero over part of each cycle. The great sensitivity of this ganglion cell is indicated by the fact that when the temporal and spatial frequencies are both approximately optimal (as they were in this experiment) a contrast of little more than 0·1 is sufficient to cause the pulse density to fall to zero for part of each cycle. Even at the lowest contrast levels, however, the wave form of the modulation of the pulse density is also clearly not sinusoidal. This is not surprising in view of the obviously non-linear relation between the amplitude of the pulse-density modulation and the contrast of the stimulus pattern. Insufficient measurements were made to define this relation well but the response amplitude was approximately proportional to the square root of the stimulus contrast. We have found no evidence at all for a threshold type of non-linearity in the stimulus–response relation for those cells which discharge spontaneously in the absence of any temporal variation of retinal illumination. These findings are in accord with those of Fitzhugh (1957), who studied the response of retinal ganglion cells to incremental flashes.

The contrast sensitivity function of X-cells

Since the initial processes of spatial summation in the cat's eye have been shown to be effectively linear for the X-cells, we can investigate and describe these initial processes by methods applicable to linear systems.

Thus, if we measure, for gratings of different spatial frequencies, the contrast required to evoke a certain fixed response from an X-cell we can derive an estimate of the relative 'contrast sensitivity function' of the cell. This will in effect be the (arbitrarily scaled) spatial contrast transfer function of the linear mechanisms involved.

Objective measurements of contrast sensitivity. Direct determination of the contrast sensitivity function of a ganglion cell can be made by recording the response of the cell to a series of gratings of different spatial frequencies each at several contrast levels. From these recordings the contrast required at each spatial frequency to evoke a response of a given magnitude can be found by interpolation. Of course, the interaction at the ganglion cell level of the summated centre and surround signals has not been shown to be linear (subtractive) even though these signals themselves (*C* and *S* of Fig. 2) appear to be the resultants of linear summation. Thus it is not necessarily possible to evoke exactly the same response even from an X-cell with gratings of different spatial frequency whatever the relative contrast levels of the gratings.

However, as can be seen from Fig. 6 which shows the responses of an X-cell to a series of gratings of different spatial frequencies and contrast, gratings of different frequencies do in fact evoke substantially the same

responses when their contrast levels are appropriately adjusted. It thus seems reasonable to assume that the interaction of the summated centre and surround signals is approximately linear for X-cells, at least at these contrast levels.

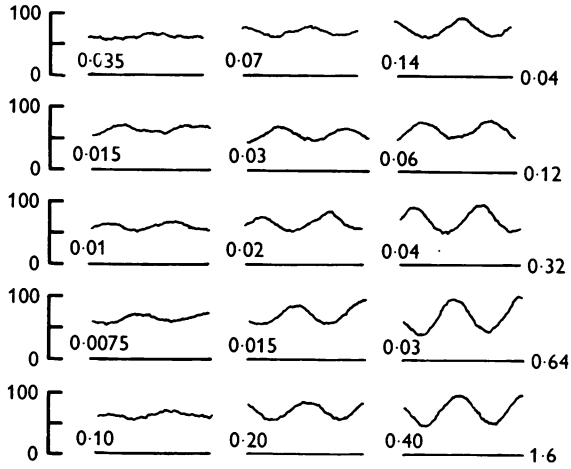

Fig. 6. Responses of an on-centre X-cell (no. 68) to a series of drifting sinusoidal grating patterns of different spatial frequencies and contrasts. The drift frequency was 4 c/s. The upper line of each pair shows the pulse density (scale at left: pulses/sec); length of the zero line represents 0·5 sec. The spatial frequency (c/deg) is shown at the right of each row and the contrast under each pulse density trace.

From the recordings shown in Fig. 6 the contrast sensitivity function of Fig. 7 was derived. The response amplitude for every contrast at each frequency was measured and plotted versus contrast. From these individual amplitude versus contrast curves the reciprocal of the contrast needed to evoke a modulation of the pulse density of amplitude 10/sec at the different spatial frequencies was obtained and are shown as filled circles in Fig. 7. The contrast sensitivity of this cell had a maximum at about 0·5 c/deg; it fell off rapidly at higher spatial frequencies and more slowly at lower frequencies.

Subjective measurements of contrast sensitivity. The objective determination of contrast sensitivity functions by this method is too time consuming to be practicable as a routine procedure and we have adopted a subjective method similar to that employed by other investigators to determine equality of response. In this method the experimenter listens to the discharge of a cell and adjusts the contrast of the stimulus pattern so that the modulation of the discharge frequency is barely detectable. Two kinds of check have been made to find whether this procedure results in an adequate determination of the contrast required to produce a constant response amplitude.

In Fig. 7 a direct comparison of objectively and subjectively determined contrast sensitivity functions for the same cell is illustrated. The sensitivity scale is essentially arbitrary for both determinations and hence the curves have been shifted relative to each other along the contrast scale to facilitate direct comparison.

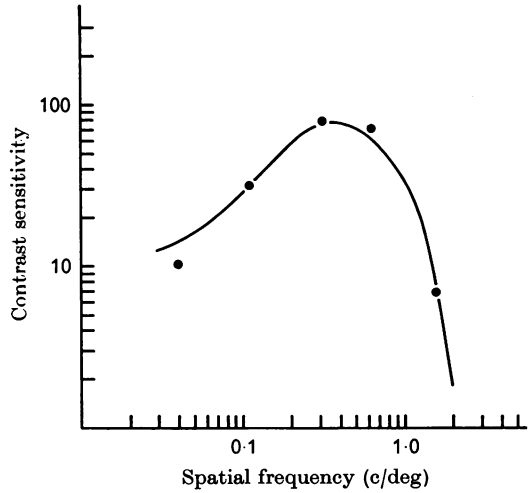

Fig. 7. Objectively and subjectively determined contrast sensitivity functions for an on-centre X-cell (no. 68). Objective measurements (filled circles): these are based on the responses of the cell to sinusoidal gratings drifting at 4 c/s (shown in Fig. 6). Response amplitude versus contrast curves were drawn for each spatial frequency and from these curves the contrast required to evoke a pulse density modulation of amplitude 10/sec was estimated. Reciprocals of these values are plotted here. Subjective measurements (continuous line): at different spatial frequencies the experimenter determined the contrast required for a barely audible modulation of the ganglion cell discharge synchronous with the drift. The reciprocals of these contrast values were plotted (Fig. 9*C*) and the experimental points were fitted with a curve conforming to eqn. (9) (p. 536). This curve is shown here.

Another type of check upon the validity of the method is to measure objectively the amplitudes of the responses previously judged by the experimenter to be at threshold. Figure 8 illustrates the results of a check of this kind. The responses of an X-cell to various gratings having twice the contrast subjectively found to produce a barely audible modulation of the impulse density are found to be very similar in amplitude though having slightly different wave forms. We also established that the repeatability of such subjective contrast sensitivity determinations for an individual cell was satisfactory even when the individual determinations were separated in time by as much as $2\frac{1}{2}$ hr. In Fig. 9 are some representative samples to illustrate this. From these various tests we conclude that the subjective method of measuring contrast sensitivity functions can be employed satisfactorily for X-cells.

Rotational symmetry of receptive fields. Kuffler (1953) found that the contours of constant sensitivity of cat retinal ganglion cell receptive fields (mapped out with a small spot of light) were approximately concentric circles. Approximate rotational symmetry of receptive fields was also found by Rodieck & Stone (1965*b*). This implies that the sensitivity of such cells to grating patterns should be independent of the orientation of the grating.

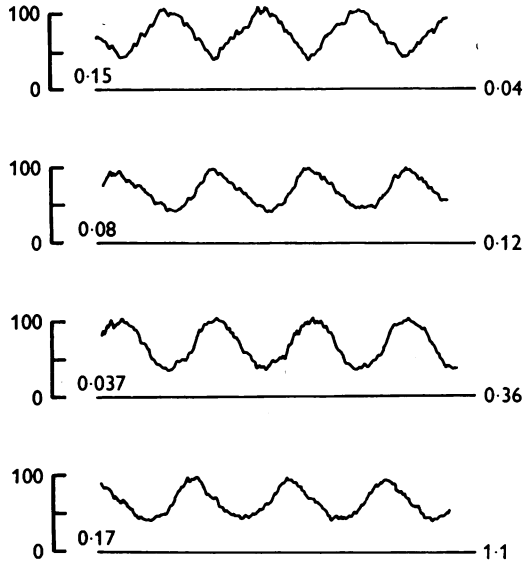

Fig. 8. Responses of an on-centre X-cell (no. 68) to sinusoidal gratings drifting at 4 c/s across the receptive field. The upper trace of each pair is the pulse density (scale at left: pulses/sec); the zero line represents 1 sec. The spatial frequency of the drifting grating pattern (c/deg, shown at the right of the records) increases from above downwards. At each spatial frequency the contrast was set to twice the value found to produce a just-audible modulation of the discharge frequency. These contrast values are given at the left of each record. Note that the peak-to-peak response amplitudes were very similar at the four different spatial frequencies, though there were slight differences in the wave forms.

Some confirmation that the contrast sensitivity function of an X-cell is independent of the orientation of the grating was provided by measurements of the contrast sensitivity function made with horizontal and vertical gratings. Figure 10 shows for an on-centre X-cell that within the precision of the measurements there appears to be no significant difference between the effectiveness of vertical and horizontal gratings. In the rabbit (Barlow *et al.* 1964) and squirrel (Cooper & Robson, 1966), retinal ganglion cells which respond selectively to the motion of patterns in some particular preferred direction are quite common. In this study it was always established

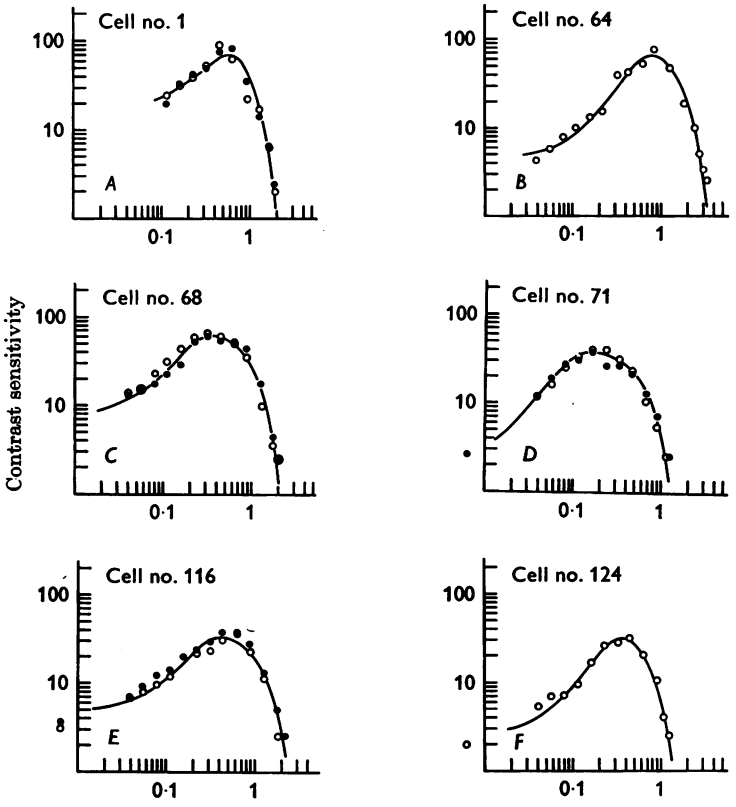

Fig. 9. Subjectively measured contrast sensitivity functions for five on-centre X-cells (*A–E*) and one off-centre X-cell (*F*). Sinusoidal grating patterns of different spatial frequencies drifted past the receptive field of each ganglion cell at a drift frequency of 1 c/s. Each point represents a single determination of the contrast which was required for the experimenter to hear a modulation of the discharge frequency at 1 c/s (i.e. synchronously with the temporal luminance modulation). Where there are two sets of symbols these represent two complete runs of contrast-sensitivity determinations each proceeding from the lowest to the highest spatial frequency. Filled circles, first determination; open circles, second determination. Time between first and second run in *A*, 40 min; in *C*, 1 hr; in *D*, 2 hr 40 min; in *E*, 1 hr 45 min. The points located to the left of the vertical axis in *D–F* indicate the contrast sensitivity at 'zero spatial frequency'. To determine this point the luminance of the *uniformly* illuminated stimulus field was modulated sinusoidally at 1 c/s and the minimum amplitude of the luminance modulation required to evoke an audible modulation of the discharge frequency was determined. The mean luminance remained the same as when the stimulus was spatially modulated. All the curves in this figure conform to eqn. (9) (p. 536), the parameters chosen being shown in Table 1. The cells can be identified by their numbers (given at the top left of the curves). Cell no. 64 had the highest spatial resolution of all cells studied.

that the cell under investigation was not selectively motion-sensitive before obtaining data with moving sinusoidal contrast patterns. No directionally selective cells were encountered, a finding which agrees well with the results of others in the cat (Rodieck & Stone, 1965*a*, *b*).

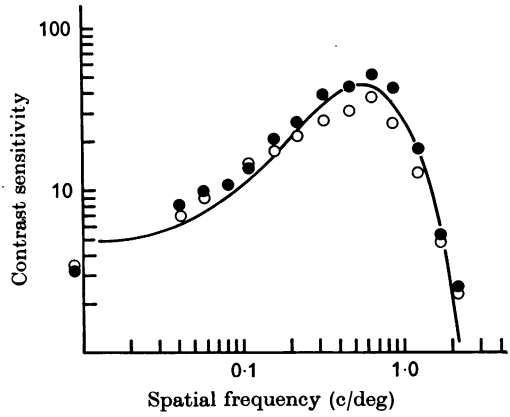

Fig. 10. Check of radial symmetry of a ganglion cell receptive field. Two subjectively determined contrast sensitivity functions for an on-centre X-cell (no. 116). Open circles: the bars of the drifting sinusoidal pattern were vertical and motion was from left to right in the cat's visual field. Filled circles: bars of pattern were horizontal and motion was from above down.

Interpretation of contrast-sensitivity functions. Before discussing the characteristics of the contrast-sensitivity functions of individual retinal ganglion cells (X-cells) and the effects upon them of changing the mean level of illumination, it is convenient to consider whether a simple analytic expression can be fitted to all the measured contrast sensitivity functions. It is clearly advantageous to be able to describe the spatial summation over each receptive field by an expression of standard form with appropriate parameters, especially if this relates in a simple manner to the sensitivity at different points over the receptive field.

We assume (cf. Ratliffe, 1965) that the response of a ganglion cell is related (not necessarily in a linear way) to R_1 where

$$R_1 = \int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty} L(x, y)\ W(r)\,dx\,dy.$$

$L(x, y)$ is the luminance over the stimulus plane and $W(r)$ is the 'point weighting factor' for a unit area at a distance r from the centre of the receptive field. By making W a function of r alone we assume perfect rotational symmetry of the receptive field.

For the simpler case in which the luminance varies in the x direction only (i.e. a 'line' pattern) the ganglion cell response is determined by R_2 where

$$R_2 = \int_{-\infty}^{+\infty} L(x)\omega(q)\,dx. \tag{1}$$

$L(x)$ is the luminance along the line at x and $\omega(q)$ is the 'line weighting function' for a strip of unit width at a distance q from the centre of the receptive field.

The line and point weighting factors can be related:

$$\omega(q) = 2\int_{q}^{\infty} \frac{W(r)\,r}{\sqrt{(r^2-q^2)}}\,dr. \tag{2}$$

Now consider a ganglion cell stimulated by a sinusoidal grating pattern whose luminance $L(x)$ is defined by

$$L(x) = L_0(1 + m\cos 2\pi\nu x),$$

where m is the contrast of the grating, ν its spatial frequency (c/unit x) and L_0 its mean luminance. In this case the cell responds to R_3 where, from eqn. (1),

$$R_3 = \int_{-\infty}^{+\infty} L_0[1 + m\cos(2\pi\nu q + \phi)]\,\omega(q)\,dq,$$

ϕ being the distance from the centre of the receptive field to the origin of x expressed as a phase angle (at the spatial frequency ν). Then, taking into account the symmetry of $\omega(q)$ about $q = 0$,

$$R_3 = 2L_0\int_0^{\infty} \omega(q)\,dq + 2Lm\cos\phi\int_0^{\infty}\omega(q)\cos 2\pi\nu q\,dq.$$

But

$$2\int_0^{\infty}\omega(q)\cos 2\pi\nu q\,dq = C(\nu) \tag{3}$$

can be identified as the cosine (Fourier) transform of the line weighting function so that

$$R_3 = 2L_0\int_0^{\infty}\omega(q)\,dq + L_0 m\cos\phi\,C(\nu). \tag{4}$$

If the grating moves at constant velocity so that

$$\phi = 2\pi ft,$$

where f is the temporal frequency of the motion ('drift frequency') and t is time then, substituting in equation (4), gives

$$R_4 = 2L_0\int_0^{\infty}\omega(q)\,dq + L_0 m\cos 2\pi ftC(\nu). \tag{5}$$

In the experimental investigation, determinations were made for each ganglion cell of the contrast m' required at different spatial frequencies to produce a particular amplitude of modulation of the pulse density of the discharge. These determinations were used to estimate the contrast sensitivity function $S(\nu)$ thus:

$$S(\nu) \propto \frac{1}{m'(\nu)}. \tag{6}$$

Assuming that a constant amplitude of the modulation of the pulse density is equivalent to a constant amplitude of modulation of R_4 then, from eqns. (5) and (6),

$$S(\nu) = KC(\nu), \tag{7}$$

where K is an arbitrary constant determined by the chosen amplitude of modulation of the pulse density. The contrast sensitivity function of a ganglion cell can thus be interpreted in terms of the cosine transform of its line-weighting function.

It is convenient to assume an analytic form for the point-weighting function of a ganglion cell and then to derive from this the line-weighting function and contrast sensitivity function of the cell. In general agreement with previous authors (e.g. Schade, 1956; Rodieck, 1965) we assume that the point-weighting functions of both centre and surround summating regions of a typical ganglion-cell receptive field are Gaussian in form and that the signals from these regions subtract arithmetically, i.e.

$$\begin{aligned} W(r) &= W_c(r) - W_s(r) \\ &= k_c\exp[-(r/r_c)^2] - k_s\exp[-(r/r_s)^2], \end{aligned}$$

where the subscripts c and s refer to the centre and surround summating regions of the receptive field, these regions having respectively characteristic radii r_c and r_s and point-weighting functions with maximum values of k_c and k_s (see Fig. 2).

The line weighting function is given by

$$\omega(q) = \omega_c(q) - \omega_s(q),$$

and then from eqn. (2)

$$\omega(q) = k_c r_c \pi^{\frac{1}{2}} \exp[-(q/r_c)^2] - k_s r_s \pi^{\frac{1}{2}} \exp[-(q/r_s)^2] \quad (8)$$

and from eqn. (7) the contrast sensitivity function

$$S(\nu) = K\pi\{k_c r_c^2 \exp[-(\pi r_c \nu)^2] - k_s r_s^2 \exp[-(\pi r_s \nu)^2]\}. \quad (9)$$

Thus it can be seen that if the point-weighting function of a ganglion cell is the difference of two Gaussian pulses then so also is the line-weighting function, and the contrast sensitivity function is the difference of two Gaussian spectra.

To see if the measurements of contrast sensitivity at different spatial frequencies could be fitted by curves conforming to eqn. (9), families of such curves with various ratios of r_s/r_c and $k_s r_s^2/k_c r_c^2$ were plotted in double logarithmic co-ordinates. These were compared (by eye) with the measured values of contrast sensitivity plotted in similar co-ordinates for each of the X-cells encountered. By suitable displacement of the curves relative to the experimental points, it was always possible to select a curve which fitted satisfactorily.

TABLE 1. Parameters of curves (conforming to eqn. 9) selected to fit contrast sensitivity measurements for X-cells

Cell no.	r_c(deg)	r_s(deg)	r_s/r_c	$k_s r_s^2/k_c r_c^2$
1	0·32	0·76	2·4	0·92
40	0·37	2·2	5·9	0·90
43	0·53	1·6	3·0	0·95
55	0·21	1·4	6·5	0·78
56	0·14	3·3	23	0·98
57	0·20	1·4	7·1	0·73
64	0·16	0·91	5·7	0·94
66	0·49	3·3	6·8	0·80
68	0·29	1·6	5·5	0·90
70	0·29	2·4	8·5	0·98
71	0·49	3·6	7·5	0·93
79	0·64	6·4	10	0·90
83	0·42	1·8	4·2	0·93
84	0·88	2·5	2·9	0·95
96	0·40	4·0	10	0·87
98	0·20	2·9	11	0·95
101	0·64	4·0	6·3	0·86
112	0·45	1·6	3·6	0·88
116	0·24	0·96	4·0	0·96
124	0·40	1·6	3·8	0·95
128	0·37	1·5	3·9	0·90

Cells 84, 101, 112 and 124 had off-centres, all the others had on-centres. The mean luminance of the stimulus screen was 16 cd/m². A 3·5 mm diameter pupil was used with all cells except nos. 43, 55, 84, 101 and 124.

Measured contrast sensitivity functions. Satisfactory measurements were made of the contrast sensitivity functions for twenty-one X-cells (seventeen on-centre and four off-centre units). Examples of these measurements and of the fit of the selected curves can be seen in Fig. 9. Table 1 gives the values of the parameters which define the shape of the fitted contrast-sensitivity functions. We have omitted giving the values for all four parameters independently because unfortunately objective determinations of

the sensitivities of most of the cells were not made and thus the relative positions of the different curves along the sensitivity axis depend upon the subjective criterion of response adopted by the experimenter for each determination. Although not directly investigated, it seems very likely that there would be appreciable variation in the citerion chosen on different occasions according to the mean discharge frequency of the individual cells. Even at the one luminance level at which the parameters of Table 1 were obtained the mean impulse frequencies of the ganglion cells involved ranged between 10 and 100 impulses/sec.

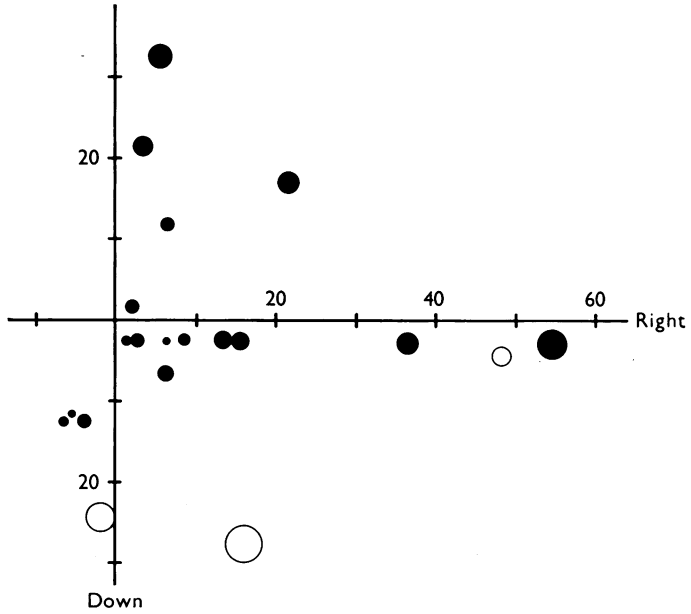

Fig. 11. Approximate visual field locations of the receptive field centres of twenty X-cells whose axons ran in the left optic tract; these are the cells listed in Table 1 except for one off-centre cell (no. 112) whose location was not recorded. The positions of the receptive field centres relative to the projection of the middle of the area centralis were estimated to within 5 deg. The axes are marked in angular distance (deg) from the projection of the centre of the area centralis. Filled circles, on-centre cells; open circles, off-centre cells. The diameter of each symbol is equivalent to 5 times the characteristic radius of the central summating region of the receptive field.

Despite the wide variation in the parameters of the contrast-sensitivity functions of the various ganglion cells it is clear that the parameters chosen to define the ganglion-cell receptive fields are partially correlated. For example, the variation in the ratio of the total weights of centre and surround summating regions ($k_s r_s^2 / k_c r_c^2$) is obviously much less than that of the individual parameters.

Figure 11 shows how the X-cell receptive fields were distributed over the visual field. The size of the symbols plotted indicates the relative size of the centre summating regions of the receptive fields. Wiesel (1960) stated that 'ganglion cells with small field centres were most often recorded in the area centralis' and that 'larger field centres were more common for ganglion cells recorded in the periphery of the retina'. For our sample of X-cells the same seems to hold true.

Sensitivity of a cell to a contrast edge

The sensitivity of a ganglion cell to patterns other than sinusoidal gratings should be calculable from a knowledge of its contrast sensitivity function assuming that the superposition principle is applicable. As an independent check of the applicability of the superposition rule we examined the responses of an X-cell to a simple contrast edge pattern and have compared the cell's measured sensitivity to the edge with the sensitivity predicted from the contrast sensitivity function.

A voltage having a rectangular wave-form and a zero mean was used to modulate the luminance of the screen of the cathode-ray tube which provided the stimulus. The presence of the modulating voltage caused the luminance of one half of the screen to increase and the luminance of the other to decrease by an equal amount. The two halves of the screen were divided about a vertical straight edge whose distance from the centre of the screen could be altered. The modulating voltage was switched on and off at 0·45 c/s and the pattern consequently appeared and disappeared at this frequency.

Figure 12 shows responses of an on-centre X-cell to the introduction and withdrawal of the edge pattern for various positions of the edge with respect to the centre of the receptive field. It is clear that the magnitude of the response depends upon the position of the edge, that the polarity of the response changes as the edge is moved from one side of the receptive field centre to the other and that when the edge is in the centre, i.e. when it forms a diameter of the receptive field, there is virtually no response at all. The existence of a position for the edge in which changes in contrast do not evoke a response from the cell provides confirmation of the linearity of the processes of spatial summation occurring over the receptive field of this X-cell.

For various positions of the edge it was possible to determine what contrast had to be introduced or withdrawn to produce an audible increase in the discharge frequency of this cell. The results of this determination are shown in Fig. 13. The contrast sensitivity of the cell for the edge pattern is shown as a function of the distance of the edge from the receptive field centre. The sensitivity was least when the edge passed through the centre of the receptive field, and greatest when it lay on either side of the centre. Also shown in Fig. 13 is the sensitivity of the cell to the edge pattern

calculated from its contrast sensitivity function previously determined with drifting sinusoidal grating patterns. The calculation has been performed by convoluting the line weighting function of the cell (Fig. 13 at bottom) with the luminance distribution in the stimulus pattern for different positions of the pattern. The equation of the cell's line weighting function was assumed to be of the standard form (eqn. (8)) and the parameters were

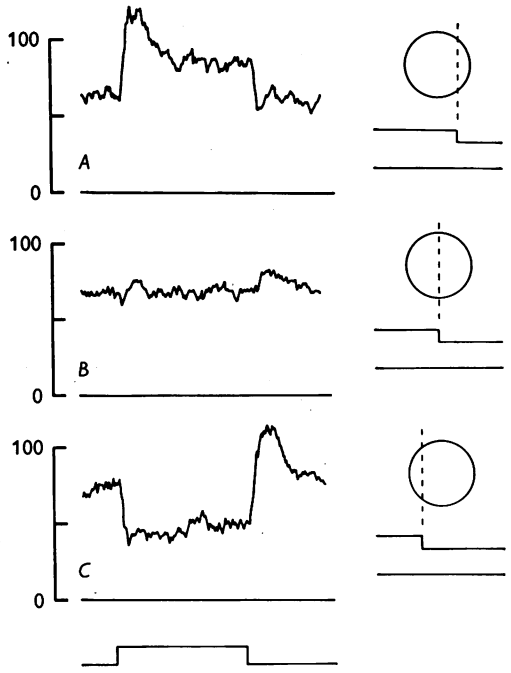

Fig. 12. Response of on-centre X-cell (no. 68) to introduction and withdrawal of an edge pattern. The edge was vertical and its contrast was 0·2. It was held stationary in three different positions while the contrast was turned on and off at 0·45 c/s. Upward deflexion of the lowest trace indicates introduction of the edge pattern, downward deflexion indicates its withdrawal. The upper line in each pair is the pulse density (scale at left: pulses/sec); the length of the zero line indicates a duration of 2 sec. The three positions of the edge relative to the receptive field centre are indicated in the sketches to the right of the records. In *A* the edge was located 7·5 min to the right of the mid point of the receptive field centre, in *B* it passed through the mid point, in *C* the edge was displaced 7·5 min to the left. The records show average responses to twenty stimulus presentations.

derived from fitting a curve of the form of eqn. (9) to the contrast sensitivity measurements (see Fig. 9*C*). Allowing for an apparent slight asymmetry in the effect of moving the edge from one side of the centre to the other, the fit can be regarded as satisfactory and as justifying the application of a linear analysis.

This ganglion cell had a rather well maintained response to the pre-

sentation of a stationary edge pattern and, for various positions of the edge, measurements were made of the average pulse density of the discharge over the period between 10 and 20 sec after introducing the pattern. In Fig. 14 the average pulse density of the discharge has been plotted as a function of the distance of the edge from the centre of the receptive field for two contrast levels. When the edge was positioned in the centre of the

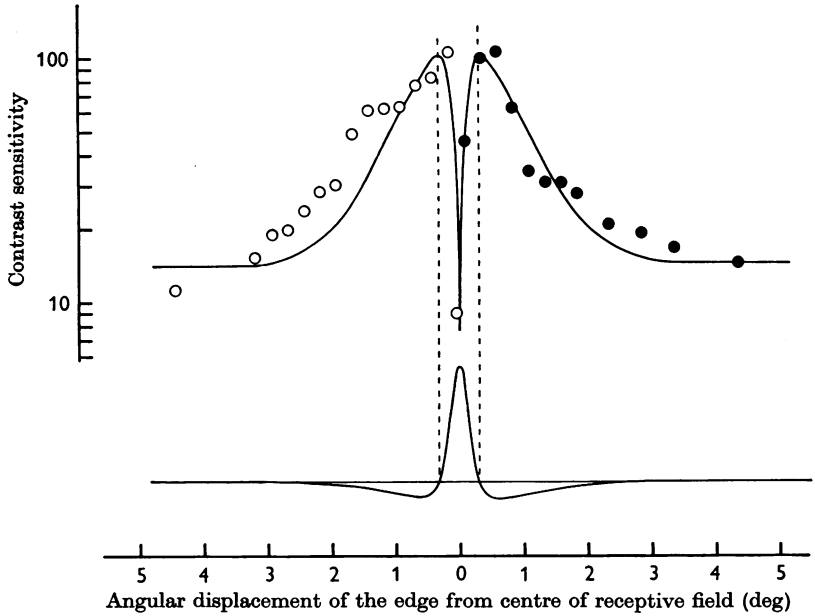

Fig. 13. Contrast sensitivity of an on-centre X-cell for an edge pattern. This is the same cell as in Fig. 12 (no. 68). A vertical edge was alternately introduced and withdrawn at 1 c/s while held stationary in different positions. For each position the minimum edge contrast which resulted in a just-audible change in the discharge frequency was determined. The reciprocals of these contrast values are plotted here. The open circles indicate responses of one polarity (Fig. 12*C*), the filled circles indicate responses of opposite polarity (Fig. 12*A*). Note the reversal of response polarity at the midpoint of the receptive field. The full line through the points is the edge contrast sensitivity of this cell calculated from its previously determined contrast sensitivity function for sinusoidal grating patterns (Fig. 9*C*). At the bottom is shown the line weighting function of the receptive field also calculated from the contrast sensitivity function.

field no effect on the cell's discharge was produced while the maximum change in pulse density was obtained when the edge was a short distance (about 0·3 deg) to either side of the centre. It is interesting to note that the maximum increase in the pulse density of the discharge was larger than the maximum decrease. If the *response* of the cell (in terms of the change in the mean pulse density of its discharge) had been proportional

to its *sensitivity* then the relative response for different edge positions calculated from the measured contrast sensitivity function and the experimentally determined response should have been the same. In fact the way in which the mean pulse density depended upon the edge position was quite similar to what would have been expected assuming linearity. This can be seen by comparing the experimental points of Fig. 14 with the full curve which shows the expected response based upon the contrast-sensitivity function measurements.

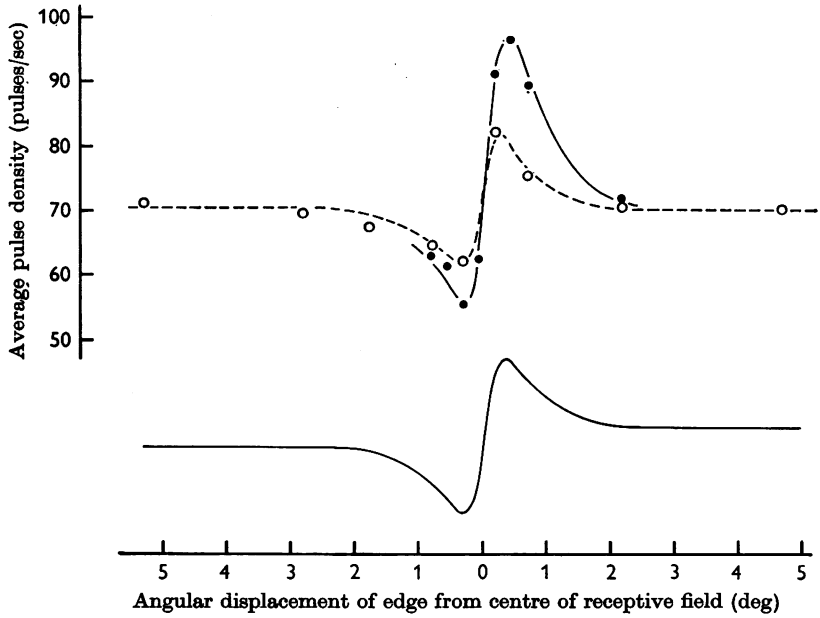

Fig. 14. 'Static' response of an on-centre C-cell to a contrast edge. This is the same cell (no. 68) as in Figs. 12 and 13. The vertical edge was held stationary at different distances from the receptive field centre and the contrast was alternately turned on and off. The average pulse density over the period 10–20 sec after the introduction of the edge was measured for each edge position. Two different contrast levels were used: filled circles, 0·4; open circles, 0·2. The edge sensitivity of the same cell calculated from the contrast sensitivity function obtained with sinusoidal gratings (Fig. 9*C*) is shown below the experimental results for comparison.

Mean level of illumination

For two X-cells the effects of changing the mean level of illumination were studied. The retinal illumination was varied by placing different neutral density filters in front of the cat's eye, ensuring that stray light did not enter the eye behind the filter. On placing a filter in front of the eye (or on taking one away), there was a marked transient change in the mean discharge frequency. After a few minutes the discharge frequency

reverted in both cases to approximately its previous level (Kuffler, Fitzhugh & Barlow, 1957). When the cell that was being studied had adapted to the new level of illumination the contrast sensitivity function was determined in the usual way. Figure 15 shows the effect upon the contrast sensitivity function of an X-cell of changing the mean illumination. Each reduction results in a decrease in the contrast sensitivity, especially at higher spatial frequencies. The other cell studied behaved in a similar manner.

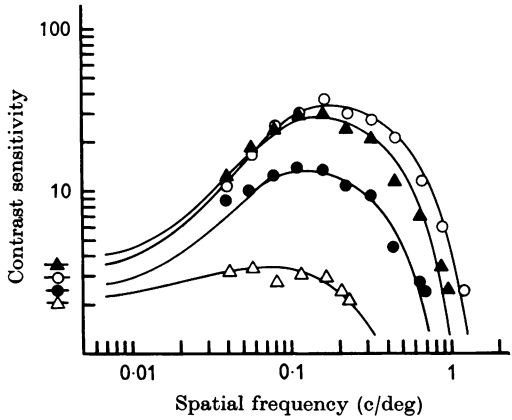

Fig. 15. The effect upon the contrast sensitivity function of an on-centre X-cell (no. 71) of changing the mean retinal illumination. The contrast sensitivity function was subjectively measured at four luminance levels of the stimulus screen: ○, 16; ▲, 0·5; ●, $1{\cdot}6 \times 10^{-2}$; △, 5×10^{-4} cd/m^2. The pupil diameter was 3·5 mm in each case.

Clearly the shape of the contrast sensitivity function changes as the illumination changes. The fall-off in sensitivity at low spatial frequencies disappears at reduced illumination levels. This can be interpreted as a disappearance of the effect of the antagonistic surround of the cell's receptive field at low light levels as described by Barlow *et al.* (1957). It is not possible, however, to fit the experimental points satisfactorily by a series of curves of standard form (eqn. 9, p. 536) which differ only in the maximum values of the weighting functions of centre and surround summating regions (i.e. which have different values of k_c and k_s). To achieve a satisfactory fit in the high-frequency region it is necessary to assume that decreasing the mean illumination not only decreases k_c and k_s but also increases the characteristic radius of the centre summating region (r_c). Over the range of illumination studied here (4·5 log. units) a 2-fold change in r_c is required to fit the results.

It also seems necessary to assume that there is a similar change in the characteristic radius of the surround summating region. The curves in

Fig. 15 have in fact all been drawn with $r_s/r_c = 9$, but though the fit is satisfactory it is not critically dependent upon this parameter.

'Contrast-sensitivity functions' of Y-cells

Although the use of contrast-sensitivity functions to describe the spatial characteristics of retinal ganglion cells can only be fully justified for those cells which demonstrate linear spatial summation (X-cells), it is, of course, possible to determine what contrast is required for gratings of different spatial frequencies to produce a given effect upon Y-cells. There are, however, two distinct effects to be considered: an increase in the mean

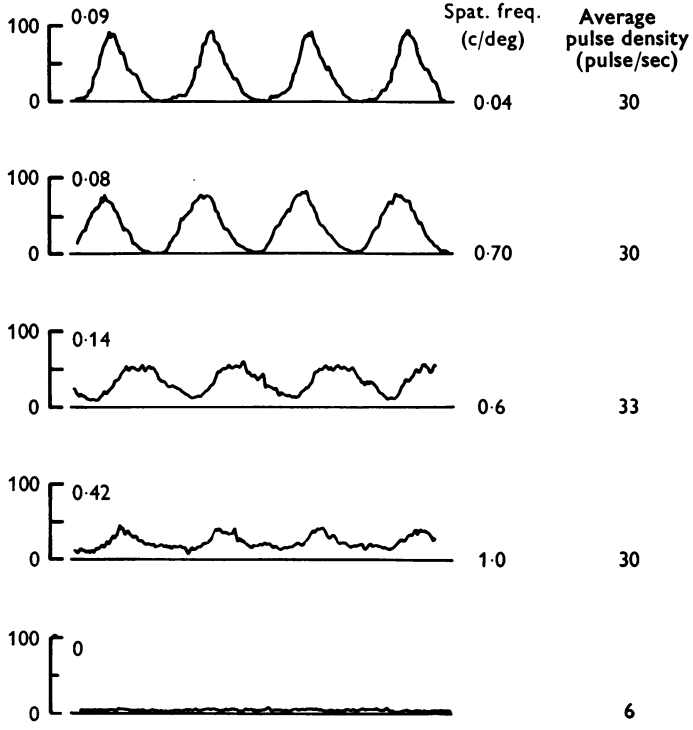

Fig. 16. Responses of an off-centre Y-cell (no. 103) to drifting sinusoidal grating patterns of different spatial frequencies. Upper line in each pair is the pulse density (scale at left: pulses/sec); the length of the zero line represents 1 sec. Drift velocity 4 c/s. The lowest record is the response to a uniformly illuminated field. Four spatial frequencies were chosen and for each frequency the contrast was adjusted so as to yield as nearly as possible the same mean pulse density. The contrasts required are given at the left of the records. The mean pulse densities that were achieved during the experiment are given at the extreme right of the figure. Note that the amplitude of the pulse-density modulation is greater at low spatial frequencies even though the mean pulse density is increased by the same amount at all frequencies.

impulse density and a modulation of the impulse density predominantly at the drift frequency of the stimulus. But these two effects do not go hand-in-hand, as is demonstrated in Fig. 16. Gratings with different spatial frequencies whose contrasts have been chosen to produce the same increase in the mean pulse density obviously do not all produce the same amplitude of modulation of the pulse density, the dominant effect at high spatial frequencies being the increase in mean pulse density. There is thus no unique contrast sensitivity function for a Y-cell. However, it is possible using the subjective method to make consistent determinations of two relations between contrast and spatial frequency for Y-cells. These two

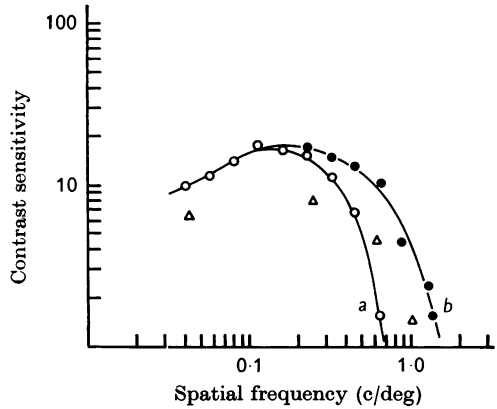

Fig. 17. 'Contrast sensitivity' of an off-centre Y-cell (no. 103, same as in Fig. 16) for sinusoidal grating patterns. The procedure was similar to the subjective measurement of the contrast sensitivity function for an X-cell. For each spatial frequency, the experimenter determined (*a*) the contrast required for an audible modulation of the discharge frequency of the cell synchronous with the temporal luminance modulation; the reciprocals of these contrast values are plotted as open circles. He also determined (*b*) the contrast required for an audible increase in mean discharge frequency as the grating was set in motion. The reciprocals of these contrast values are plotted as filled circles. The triangles are the reciprocals of the contrasts required to increase the mean discharge frequency of the cell from 6 to 30 impulses/sec. These values are taken from Fig. 16.

relations are obtained when the experimenter finds for each spatial frequency what contrast is required for him to detect either a periodic modulation of the pulse density of the discharge of the cell or an increase in the mean pulse density when the grating is set in motion. The two contrast-sensitivity relations determined in this way differ considerably at high spatial frequencies (Fig. 17) as would be expected from the effect illustrated in Fig. 16. The contrast sensitivity as judged by the effect of a drifting grating upon the mean impulse density is relatively greater at higher frequencies. In Fig. 17 the contrast-sensitivity curves obtained when using the two different subjective criteria for threshold contrast are

shown and for comparison four objective determinations of the contrast needed to evoke an increase in the mean pulse density of 25/sec.

Receptive field centres of Y-cells tended to be larger than those of X-cells (centres of both types mapped with the same small flashing light) and Y-cell centres had less tendency than X-cell centres to be located centrally in the visual field. This makes it likely that Y-cell axons generally are larger than X-cell axons. Possibly this explains why some of our electrodes only recorded the discharges from Y-cells.

DISCUSSION

Spatial summation in the retina

Linear summation. In our experiments with stationary patterns it was found that for certain ganglion cells (designated X-cells) in the cat's retina a decrease in the illumination over one half of a receptive field could completely nullify the effect of simultaneously increasing in the same way the illumination over the other half of the receptive field. Upon this observation we primarily base our conclusion that the signals from photoreceptors in the cat's retina are effectively linearly related to the incident illumination and that the signals from photoreceptors in both the centre and surround summating regions of an X-cell receptive field add linearly before they affect the discharge of the ganglion cell.

Barlow (1953) demonstrated approximate linearity of addition over the receptive field centres of some frog ganglion cells though he did not consider the interaction of simultaneous increments and decrements of luminance in different parts of a receptive field. Barlow also demonstrated that, for a ganglion cell with a concentric type of receptive field, the luminance of a peripherally positioned spot which just inhibited the effect of a central one was linearly related to the luminance of the central spot. He concluded that this indicated approximately linear action in the inhibitory surround region of a receptive field as well as in the central region. It should be noted that Barlow's conclusion that there is linear addition of signals in the retina was based upon measurements of the *sensitivity* of ganglion cells; that is, upon finding stimuli that were equivalent to each other in producing a certain response from a cell. Barlow did not claim, and we make no claim, that the *response* of a ganglion cell is linearly related to the stimulus magnitude. Moreover, Barlow does not provide evidence for asserting that the interaction between summated signals from centre and surround regions is subtractive. It seems that the assumption of a divisive process of interaction would be equally consistent with his experimental results and ours.

Rodieck (1965), on the other hand, assumed that the principle of super-

position could be applied in interpreting the *responses* of cat retinal ganglion cells to various stimuli (Rodieck & Stone, 1965*a*, *b*). In our experience, however, even for those cells (X-cells) with receptive fields over which the initial process of spatial summation appears to be linear there are always signs of markedly non-linear behaviour evident in the relation between stimulus and response amplitudes. This non-linear relation appears to hold down to very low contrast levels and suggests that there is a fundamentally non-linear mechanism in the retina. It is interesting to note that in experiments with drifting sinusoidal gratings the distortion of the wave form of the modulation of the pulse density of the discharge of the responding cell does not appear to be reduced as the contrast of the stimulus approaches zero; indeed, in some instances it even probably increases.

In our analysis of spatial summation over the receptive fields of X-cells we have assumed (with Rodieck, 1965) the existence of separate processes of summation in the central and surround regions of the receptive fields. We have also assumed that the sensitivities of both centre and surround summating regions fall off as Gaussian functions of the distance from the middle of the receptive field. Our only justification for making these assumptions is that they lead to a particularly simple mathematical formulation of the process of spatial summation which gives a satisfactory fit with our experimental results.

In the interpretation of the measurements of the contrast-sensitivity function of ganglion cells it has been assumed that the effects of the optics of the cat's eye are negligible. In particular the fall-off in sensitivity at high spatial frequencies has been assumed to result from spatial integration in the retina rather than from optical blurring. Support for this assumption comes from Westheimer's (1962) measurements of the ophthalmoscopically observed fundal image in a cat's eye. These measurements indicate that even with a 6 mm diameter pupil little attenuation of contrast occurs at spatial frequencies below 2 c/deg. With a smaller pupil even less contrast attenuation would be expected as most of the (in-focus) blurring can probably be ascribed to spherical aberration (Morris & Marriott, 1961). With a small pupil also the effects of focus errors are minimized; in any case these are relatively slight at the relevant spatial frequencies and are unlikely to have contributed significantly to the measured fall-off in contrast sensitivity at the higher spatial frequencies.

Non-linear summation. On the basis of experiments with drifting grating patterns whose spatial frequency approached the upper limit at which the retinal ganglion cells would still respond we classified the cells into two types: Y-cells whose response was evident as an increase in the mean pulse density of their discharge and X-cells whose response was evident as a modulation of their pulse density at the drift frequency. We never

had any difficulty in distinguishing between these two cell types. The Y-cells were also characterized by the impossibility of finding for them any position for a grating of low spatial frequency in which the pattern could be turned on or off without evoking a response. Upon the latter observation we base our conclusion that Y-cells do *not* respond to the sum of signals proportional to luminance coming from all parts of their receptive fields. This direct test for non-linear action was not applied to all those ganglion cells classified as Y-cells on the basis of their response to drifting gratings. However, in every case where it was applied it gave the same result. No other consistent differences in the behaviour of X- and Y-cells were observed.

Whether our classification of ganglion cells into two distinct classes would be upheld by objective measurements of the detailed behaviour of a large sample of ganglion cells under a wide range of conditions (e.g. of mean luminance) cannot be answered, but there can be no doubt that under the conditions of our experiments there was a very big difference in the behaviour of typical members of the two classes.

Diameter of receptive fields

From our measurements of the contrast sensitivity of X-cells to sinusoidal grating patterns of different spatial frequencies it has been possible to calculate the characteristic radius, r_c, of the central summating region of the receptive fields of these cells; r_c is the radius at which the sensitivity of the central summating region falls to $1/e$ (37 %) of its maximum value. Conventionally, however, the diameter of the central region of a receptive field is equated either with the diameter of the disk of light which has the lowest increment threshold (e.g. Wiesel, 1960) or with the diameter of the boundary between the receptive field regions from which responses of opposite polarity can be evoked by a small spot of light. In our formulation the radius of the conventional receptive field centre, r_c', is the radius at which the sensitivities of central and surround summating regions are equal, i.e. $W_c(r_c') = W_s(r_c')$. Using this relation we have calculated the diameter of the conventional centres of our sample of twenty-one X-cells. The range was 0·55–2·9 deg as compared to 0·5–4 deg reported by Rodieck & Stone (1965*b*) for all retinal ganglion cells from which they recorded. The modal value of the diameters in our sample was between 1 and 1·5 deg which is in accord with the value found by Wiesel (1960) recording directly from the retina with micropipettes. In Wiesel's experiments the retinal illumination was probably 2–3 times greater than in ours.

In relating the diameters of receptive field centres to the histologically determined structure of the cat's retina, Brown & Major (1966) compared the diameters of ganglion-cell dendritic fields with the diameters of con-

ventional receptive field centres as reported by Wiesel (1960) and Rodieck & Stone (1965*b*). If the partial coextension of centre and surround summating regions is accepted, then dendritic field diameters might more reasonably be related to the diameters of the central summating regions than to the diameters of the conventional field centres. Since the sensitivity of each centre summating region is assumed to fall off continuously from its maximum value these regions do not have a well-defined diameter, but a value of 5 times the characteristic radius (Fig. 2) probably provides a fair estimate of their anatomical diameter. Using this factor the diameters of the central summating regions of the twenty-one X-cells which were studied ranged from 0·7 to 4·5 deg without any clear indication of the bimodal distribution reported by Brown & Major (1966) for the diameters of ganglion-cell dendritic fields. It is interesting to note, however, that the central summating region of no X-cell significantly exceeded the diameter of the largest dendritic fields. The diameters of the surround summating regions ($5\ r_s$), on the other hand, varied from a minimum of about 4 deg up to about 30 deg. Thus even the smallest surround region was as large as the largest dendritic field and most of the surround regions were much larger.

Because of the obviously non-linear behaviour of Y-cells we have not attempted to interpret measurements of their relative sensitivity to grating patterns of different spatial frequencies in terms of a linear model. We therefore do not have estimates of the diameters of the central summating regions of Y-cells comparable to those for X-cells. For many Y-cells, however, the diameter of the conventional receptive field centre was measured with a small spot of light. Diameters between 1 and 7 deg with a modal value of about 3 deg were found. These values are considerably larger than those for X-cells measured with the same small spot or calculated from their contrast sensitivity functions. Many of the Y-cells had conventional centres of greater diameter than the largest ganglion cell dendritic field (Brown & Major, 1966).

We have interpreted changes in the contrast sensitivity function of X-cells brought about by adaptation to lower mean luminance levels as indicating an increase in the diameters of centre and surround summating regions. If this interpretation is correct the rationale behind a comparison of the diameters of receptive field regions and ganglion-cell dendritic fields becomes obscure.

Visual acuity

It might be expected that the visual acuity of the cat could be related to the characteristics of its retinal ganglion cells. Unfortunately, no satisfactory behavioural measurement of the visual acuity of the cat has been reported. Smith (1936) found that cats could distinguish (though not per-

fectly) between vertical and horizontal gratings composed of equal width black and white bars at a spatial frequency of 5·5 c/deg when the mean luminance was probably about 250 cd/m^2 (our estimate from Smith's description). Although Smith did not use higher frequency gratings it seems likely that the cat's resolution limit was not much higher than 5·5 c/deg, at which frequency the performance of the animals appears to have been appreciably impaired.

Before comparing Smith's results with our findings it is important to note that his observations were made on cats with natural pupils. From Kappauf's (1943) data on the relation between pupil width and environmental luminance it seems likely that Smith's cats had pupil widths of a little less than 2 mm; the retinal illumination of these cats was therefore probably about 5 times higher than the maximum achieved in our experiments with a 3·5 mm diameter pupil, and the retinal image in Smith's cats may have been a little sharper than in our experiments.

Figure 9*B* shows the contrast sensitivity function of the retinal ganglion cell which responded at the highest spatial frequency. By extrapolation it can be estimated that this cell would have produced a detectable response to a square-wave grating with a contrast of 1 (equivalent to a sinusoidal grating with the same spatial frequency and a contrast of 1·27) at spatial frequencies of up to about 4 c/deg. Allowing for the difference in pupil size and retinal illumination this cell might well have produced a detectable response at 5·5 c/deg under conditions similar to those of Smith's (1936) experiments. This makes it seem unlikely that ganglion cells with much smaller centres than that of the cell of Fig. 9*B* (r_c = 0·16 deg, corresponding to a conventional centre diameter of 0·55°) are present in the cat's retina. It is, of course, difficult to assess the relation between the stimulus which will evoke from a ganglion cell a response that can be detected by an experimenter listening to its discharge and the stimulus which will produce a certain behavioural effect.

Psychophysical correlates

The contrast sensitivity function of the human visual system is derived from psychophysical measurements of the minimum contrast required for a subject to detect sinusoidal gratings of different spatial frequencies. The contrast sensitivity function for central vision has been shown to be partly determined by the dioptric mechanism of the eye and partly by neural mechanisms (see Campbell & Green, 1965). It has not, however, been possible to decide by direct experiment on humans to what extent the neural mechanisms involved are retinal. It is therefore of interest to compare the psychophysical results with the contrast sensitivity function of retinal ganglion cells as determined from animal experiments.

Assuming that the human retina is similar to the cat's the problem immediately arises whether the psychophysical measurements reflect the behaviour of retinal ganglion cells of the X- or Y-types. Since X-cells have been found to occur predominantly in the more central regions of the retina and the Y-cells predominantly in the more peripheral regions it seems possible that central human vision may be mediated by ganglion cells of the X-type. This interpretation is supported by some evidence that the psychophysically measured contrast sensitivity function (for central vision) is determined by a linear mechanism (Robson & Campbell, 1964). Moreover, Merchant (1965) has noted certain characteristics of human peripheral vision and suggested that it may be mediated by a mechanism whose behaviour would bear a close resemblance to that of Y-cells.

The form of the contrast sensitivity function of a typical X-cell (Fig. 9) resembles that of the human visual system (e.g. Schade, 1956) in that it shows a rapid fall-off at high spatial frequencies and a less rapid fall-off at spatial frequencies below some optimum value. It must be noted, however, that the form of the human contrast sensitivity function at low spatial frequencies is dependent upon the temporal frequency at which the observations are made (Robson, 1966).

It is difficult to compare in absolute terms the contrast sensitivity of a human subject with the contrast sensitivity of a ganglion cell which does not exhibit a threshold non-linearity. However, the discharge of many of the X-cells from which we recorded was clearly modulated (so as to be obvious to an experimenter listening to the discharge) by grating patterns of optimal spatial frequency and contrast of little more than 0·01. At the same retinal illumination a human subject can see grating patterns when the contrast is about 0·005. Thus it seems likely that a cat can detect patterns at contrast levels comparable to those required by a human subject.

An obvious difference between the human contrast sensitivity function and the contrast sensitivity function of any of the cat retinal ganglion cells that we have studied is that they occupy very different positions along the spatial frequency scale. The maximum observed value for the optimum spatial frequency of a cat ganglion cell was about 0·8 c/deg, while the optimum frequency for human central vision with the same retinal illumination is about 5 c/deg. The human thus seems to operate in a higher spatial frequency range than the cat. Consequently it might be expected that the human contrast sensitivity at low spatial frequencies would be less than the sensitivity of some of the cat retinal ganglion cells. Indeed in our experiments it was sometimes possible for the experimenter to detect the presence of a grating pattern by *listening* to the discharge of a cat retinal ganglion cell when he could not *see* the pattern on the stimulus screen.

Campbell & Green (1965) showed that at high spatial frequencies the human contrast sensitivity function falls off exponentially with increasing frequency while Kulikowski, Campbell & Robson (1966) have noted that it can be fitted by the difference between two exponential functions. The human contrast sensitivity function thus appears to be broader than the contrast sensitivity function of individual cat ganglion cells. It must be remembered that human contrast sensitivity at any one spatial frequency is probably determined by those ganglion cells which are most sensitive at that frequency. Thus if the human central retina contains receptive fields of different sizes the psychophysically measured contrast sensitivity function may well be broader than the contrast sensitivity functions of the individual ganglion cells. Measurement of the characteristics of cat ganglion cells support the general hypothesis that in each part of the retina there exist ganglion cells with a relatively wide size range. The existence of receptive fields of different sizes in the central human retina may also account for Campbell & Robson's (1964) observation that simultaneously presented sinusoidal grating patterns with harmonically related spatial frequencies appear to be detected independently.

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