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SPATIO-TEMPORAL INTERACTIONS IN CAT RETINAL GANGLION CELLS SHOWING LINEAR SPATIAL SUMMATION

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SUMMARY

1. The spatio-temporal characteristics of cat retinal ganglion cells showing linear summation have been studied by measuring both magnitude and phase of the responses of these cells to drifting or sinusoidally contrast-modulated sinusoidal grating patterns.

2. It has been demonstrated not only that X cells behave approximately linearly when responding with amplitudes of less than about 10 impulses/sec to stimuli of low contrast but also that cells of another type with larger receptive field centres (Q cells) behave approximately linearly under the same conditions.

3. These Q cells appear to form a homogeneous group which is probably a subset of the tonic W cells (Stone & Fukuda, 1974) or sluggish centre–surround cells (Cleland & Levick, 1974).

4. The over-all spatio-temporal frequency characteristics of cells showing linear spatial summation are not separable in space and time. The form of the *spatial* frequency responsivity function of these cells depends upon the *temporal* frequency at which it is measured while the *temporal* phase of their response measured at any constant temporal frequency depends upon the *spatial* frequency of the stimulus.

5. The behaviour of X and Q cells is quite well explained by an extension of the model in which signals from centre and surround mechanisms with radially Gaussian weighting functions are summed to provide the drive to the retinal ganglion cell. While the general form of the temporal frequency response characteristics of these ganglion cells are probably provided by the characteristics of elements common to the centre and surround pathways, the spatio-temporal interactions can be explained by assuming that the surround signal is delayed relative to the centre signal by a few milliseconds.

INTRODUCTION

Among the various ganglion cells in the cat's retina which have concentrically organized receptive fields, X cells have been characterized as showing linear spatial

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summation (Enroth-Cugell & Robson, 1966). From measurements of the sensitivity of individual X cells to drifting sinusoidal grating patterns of different spatial frequencies, Enroth-Cugell & Robson concluded that the sensitivities of the antagonistic centre and surround summating regions of the receptive fields of these cells each declined as a Gaussian function of distance from the field centre as proposed by Rodieck (1965). While these findings helped to establish a generally accepted simple functional model of the X cell receptive field and prompted the use of sinusoidal grating patterns in studying the behaviour of other visual neurones (e.g. Movshon, Thompson & Tolhurst, 1978), Enroth-Cugell & Robson's original experiments were incomplete in that they did not examine the effect of changing temporal frequency and did not include measurement of the phase of the responses. Moreover, the measurements were all made using drifting gratings and no attempt was made to see if motion of the stimulus was of any particular importance.

Improvements in technique which have been introduced since the earlier study have now made it practicable not only to compare the amplitude of a ganglion cell's responses to both drifting and contrast-modulated stationary gratings but also to measure the temporal phase of the responses with respect to the stimulus. Measurements of this kind made at a number of different temporal frequencies can provide a more complete characterization of the cell's behaviour, as well as a more critical test of receptive field models, than can be provided by measurements of response amplitude alone made at a single temporal frequency. Although the measurements we now report could be used as the basis for a complete model of the spatio-temporal behaviour of retinal ganglion cells, we have limited our aims at this stage to providing a model to explain the form of the complete spatial frequency response function (both amplitude and phase) and the way in which it changes when measured at different temporal frequencies. A further change in our technique, recording directly from retinal ganglion cells rather than from optic tract axons, has made it possible to examine the behaviour of ganglion cells with axons smaller than those of X cells. We have found that one of these other classes of ganglion cells also shows linear spatial summation.

Some of these results have been presented at the 1980 Annual Meeting of the Optical Society of America and at the 1981 Annual Spring Meeting of the Association for Research in Vision and Ophthalmology.

METHODS

Preparation. Experiments were performed on adult cats in which anaesthesia was induced either with halothane or ketamine hydrochloride (20 mg kg^{-1} intramuscularly) and continued during preparatory surgery with thiamylal sodium. Immediately after induction, 0·2 mg atropine sulphate and 4 mg dexamethasone were given intramuscularly. During the experiments anaesthesia was maintained with urethane given intravenously at a rate of 15–25 mg kg^{-1} hr^{-1} after a 100–200 mg loading dose. This rate is approximately five times higher than one that maintains light anaesthesia in unparalysed cats (Cleland & Enroth-Cugell, 1966). Some indication of the level of anaesthesia was gained from the heart rate and the blood pressure which were both continuously monitored. Mean arterial blood pressure remained above 90 mm Hg throughout the experiments although occasionally this level could only be maintained by giving intravenous methoxamine hydrochloride.

Good immobilization of the eye was achieved by a combination of mechanical stabilization (see *Recording*) and continuous intravenous infusion of gallamine triethiodide, 10–20 mg kg^{-1} hr^{-1}. After application of local atropine and, unless halothane had been used, phenylephrine hydrochloride as

well (Kirby & Schweitzer-Tong, 1981), a contact lens with a 4 mm diameter pupil was fitted to the left eye. The lens power required to bring the stimulus pattern into focus on the retina was determined by direct ophthalmoscopy and later in the experiment the correctness of focus was checked by observing whether a cell's response to a just resolvable grating pattern could be improved with additional spectale lenses. If required, such lenses were used for subsequent measurements.

Recording. Extracellular recordings were made with glass micropipettes pulled with an internal glass fibre and filled with 2 M-NaCl. Measured at 60 Hz in physiological saline these electrodes had an initial impedance of 20–50 MΩ which was reduced by bevelling to about 10 MΩ. The micropipette was directed towards different points on the retina with a mechanical micromanipulator attached to the frame of the stereotaxic apparatus in which the cat was held. This manipulator was equipped with an annular footplate 9 mm in outer diameter, through whose centre the pipette was constrained to pass as its direction was adjusted. The footplate of the manipulator was firmly glued to the carefully cleared sclera on the superior temporal aspect of the globe of the left eye about 8–9 mm behind the limbus using ethyl cyanoacrylate (Permabond no. 101). The sclera was also cleared just behind the limbus around the entire limbal circumference so that a metal ring with an internal diameter of 15 mm could be cemented to the eye. This ring, which was rigidly attached to the manipulator, not only held the eye stationary but also allowed it to be pulled forward 1–4 mm from its orbital bed to improve recording stability. After a small cautery had been used to make an opening through the sclera in the middle of the hole of the footplate, an outer guard tube was inserted into the eye and its base firmly locked onto the frame of the manipulator. A second, inner guard tube fixed to the head of a hydraulic micro-electrode drive was then slipped into the outer tube. The electrode moved in the inner of the two tubes, rubber seals preventing leakage of vitreous humour past the electrode and inner guard tube.

A fibre-optic light guide held at the cornea was used to illuminate the fundus so as to project an image of retinal landmarks onto a tangent screen on which all receptive field positions would be subsequently marked (Pettigrew, Cooper & Blasdel, 1979). The contours of the disk and the retinal vessels were traced in as much detail as possible to estimate the location of the area centralis.

Antidromic latencies. Insulated stainless-steel electrodes were stereotaxically positioned above the optic chiasm and lowered until field potentials recorded from the retinal surface were reliably evoked with stimuli (50 μsec pulses at 1–2 per second) of 2–4 V amplitude. The antidromic latencies of ganglion cells were measured from the stimulus artifact to the foot of the action potential.

Visual stimuli. The stimuli were generated by computer on a cathode-ray tube raster display (Joyce Electronics, Cambridge, England) with a 31 × 22 cm face and P-31 phosphor. The display was operated at a frame rate of 200 Hz with a line frequency of 85 kHz to give a raster with 360 lines. The cat viewed the display at a distance of 57 or 114 cm in a mirror which could be tilted about horizontal and vertical axes to centre the receptive field of the cell being studied on the mid point of the display screen. The mean (adapting) luminance of the display screen was 400 cd m^{-2}.

The stimuli we used were perturbations in space and time of the apparently steady uniform luminance L_0 of the oscilloscope screen produced by dimming or intensifying individual raster lines. The stimulus so generated can best be described in terms of the contrast of each line, contrast being defined as $(L-L_0)/L_0$, where L is the luminance of an individual line and L_0 is the mean luminance of all the lines. Note that this contrast may have a negative value. The display we used provided linear modulation of the luminance of individual lines of between 5 and 195% of the mean, to give stimuli with contrasts of up to 0·95.

Two sorts of stimulus pattern were used: sinusoidal gratings and edges. In a vertical grating of contrast m the contrast of each line was $m \cos(2\pi ux+p)$ where u is the spatial frequency, p the spatial phase of the grating relative to a reference point in the middle of the screen and x the horizontal distance of the line from that same reference point. For an edge of contrast m, the line at the centre of the sceen ($x = 0$) was set to the mean luminance, while all lines to one side were set to contrast m and all lines to the other side to contrast $-m$. As a rule, the patterns were stationary: the position of an edge, or the spatial phase of gratings relative to the middle of the screen did not vary over time. However for some experiments the stimulus was a drifting grating, i.e. the spatial phase of the grating increased linearly with time.

When stationary gratings were employed their contrast was varied sinusoidally in time by altering in each successive 5 msec frame a factor by which the signal controlling the contrast of each line was multiplied to give a 'contrast-modulated' pattern. In this case the contrast in each

line of the grating was $m \cos(2\pi wt) \cos(2\pi ux)$ where t is time, w the temporal frequency in Hz, and m the peak contrast of the pattern. As indicated by this formulation the raster lines were usually vertical, so that luminance only varied horizontally across the display and the initial spatial phase of the grating (at $t = 0$) was zero. The raster could be rotated to produce oblique or vertical variations.

Response measurement. When the stimulus is either a drifting grating or a stationary, contrast-modulated pattern, its main effect on a ganglion cell is to modulate the discharge rate at the drift or modulation frequency. However, modulation of the discharge rate at zero frequency (change in mean rate) or at frequencies harmonically related to the stimulus usually occurs to some extent as well. In our experiments we measured the amplitude of the components of the discharge rate at zero frequency as well as at the frequency of the stimulus (fundamental component of the response) and at twice that frequency (second harmonic component of the response). In the case of the fundamental the phase angle of the response relative to the stimulus (temporal phase) was also determined. These measurements were made on-line by the same computer as generated the stimuli by making a discrete Fourier analysis of the impulse train at the required frequencies. The integrations were performed over an integral number of periods of the stimulus, usually over the smallest number of periods whose total duration exceeded 10 sec. The start of the epoch during which a cell's response was analysed was always delayed for at least the longer of 1 sec or one period of the stimulus after changing any stimulus parameter so that a steady state could be reached. Although the time of occurrence of impulses was only measured to the nearest 5 msec, it can reasonably be expected that this will have had a negligible effect on measurements at frequencies up to 32 Hz (the highest frequency routinely used).

Experimental procedure and classification of cells. In this paper we deal only with cells showing linear spatial summation, although during the course of the experiments we usually also recorded from cells of other kinds. When each retinal unit was first isolated the position of its receptive field was determined using tapered white or black wands against a grey tangent screen (approximately 20 cd m^{-2}) on which this position was then marked. The location within the visual field of the receptive field of the unit could then be ascertained by reference to the previously plotted retinal landmarks. During this mapping procedure it usually became clear whether or not the recording was from a cell body or an axon, whether the cell's receptive field was centre–surround organized, whether it was linearly summating, whether it had an on- or an off-centre, and approximately how large the centre was. Assuming that the recording seemed to be from the soma (with an action potential of characteristic shape and a receptive field in the appropriate place) of a linearly summating cell, the latency of the unit's response to antidromic stimulation of the chiasm was measured.

A mirror was then placed in front of the cat and angled so that the projection of the cell's receptive field lay approximately in the middle of the display screen. Next the cat was shown a contrast-modulated vertical edge, located at the centre of the display screen. The angle of the mirror about its vertical axis was then precisely adjusted to give the smallest possible response at the temporal frequency of the contrast modulation. In this way the horizontal zero phase reference point of the stimulus pattern (always located at the centre of the screen) was made to correspond exactly to the 'middle' of the cell's receptive field. It was found that the adjustment of the mirror (and hence the accuracy of the positioning of the spatial phase reference point in the middle of the receptive field) was repeatable to better than one minute of arc over long periods of time. This indicates not only that we achieved good stabilization of the eye but also gives a good idea of how ganglion cells with quite large receptive fields can provide rather precise information about stimulus position. After this we measured the cell's response to a contrast-modulated sationary grating with spatial frequency somewhat above the optimum for the cell. From these measurements we were able to confirm linearity of spatial summation by finding that the amplitude of the second harmonic of the cell's response remained much less than that of the fundamental for all spatial phases of the grating relative to the middle of the cell's receptive field (Hochstein & Shapley, 1976). The major part of the experiment then usually consisted of measuring responses at various spatial and temporal frequencies to drifting or stationary, contrast-modulated gratings.

Phasor representation of sinusoidal responses. When driven by a stimulus with a temporal waveform $\cos(2\pi wt)$ the response of a cell at the frequency w can be written

$$r(t) = a \cos(2\pi wt + \phi) \tag{1}$$

These waveforms are sketched in Fig. 1 *A*. The stimulus has an amplitude of unity and a maximum at time zero while the response has an amplitude of a and in this example, a corresponding maximum which occurs somewhat later. A delay of the response with respect to the stimulus corresponds to ϕ, the *phase difference*, having a negative value. Such a delayed response is said to show a *phase lag*. Positive values of ϕ indicate a *phase lead*, the maxima of the response then occurring before the maxima of the stimulus. The two numbers a and ϕ which describe the response may be represented conveniently by a single complex number z which we call the *complex amplitude* of the

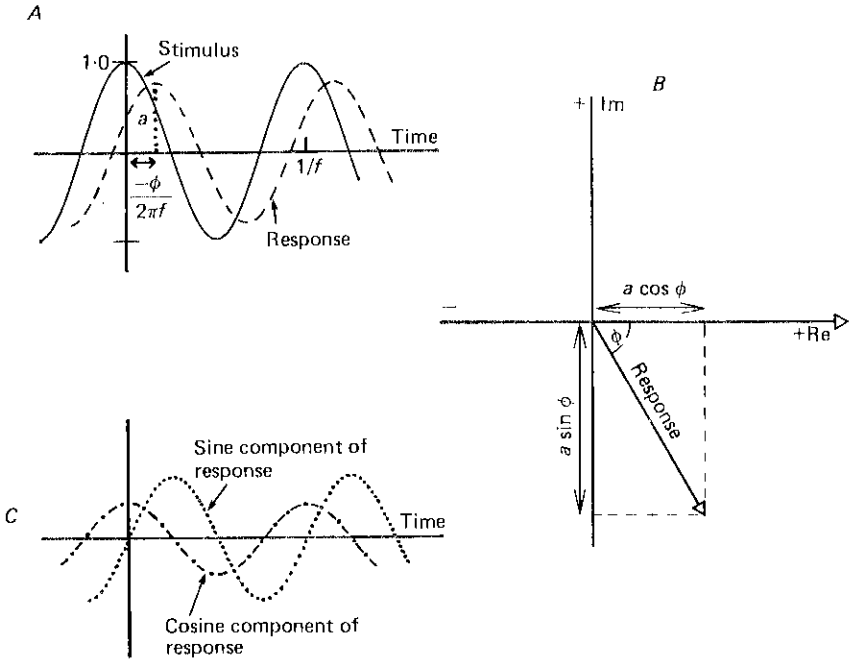

Fig. 1. Phasor representation of sinusoids. *A*, the continuous curve represents a stimulus with an amplitude of unity. The dashed curve represents a response of amplitude a which is delayed relative to the stimulus. *B*, the phasor representing the complex amplitude z of the response sinusoid. The magnitude $|z| = a$ is indicated by the length of the phasor. *C*, cosine and sine components of the response wave form in *A*. Their amplitudes are equal to the real (Re) and minus imaginary (Im) parts of the phasor in *B*.

response at frequency w. In the complex plane z is a vector with length $|z| = a$ and angle relative to the positive real axis of $\angle z = -\phi$, as shown in Fig. 1 *B*. We may also write z as a complex exponential, $z = |z|e^{i(\angle z} = ae^{-i\phi}$. The real and imaginary parts of z (its rectangular co-ordinates in the complex plane) are given by

$$\text{Re}\,[z] = |z| \cos \angle z = a \cos \phi, \tag{2}$$

$$\text{Im}\,[z] = |z| \sin \angle z = -a \sin \phi. \tag{3}$$

A trigonometric identity will show that these are simply the positive and negative amplitudes, respectively, of the cosine and sine components of the response wave form in eqn. (1). These components are shown in Fig. 1 *C*.

The complex number z, which we will call a *phasor*, is, of course, just the complex Fourier series coefficient at frequency w of the waveform in eqn. (1). A useful feature of the phasor representation is that the phasor corresponding to the sum of the two sinusoids of the same frequency is simply equal to the sum of their respective phasors. Furthermore, the product of two phasors, $z_1 z_2$, is equal to $|z_1|\,|z_2|e^{i(\angle z_1 + \angle z_2)}$. The lengths are multiplied and the angles added.

RESULTS

Our later analysis of the spatial frequency characteristics of linearly summating cells will be simplified by assuming that the behaviour of such cells can usefully be represented by a linear model. Thus we first examine what experimental justification there may be for such an assumption.

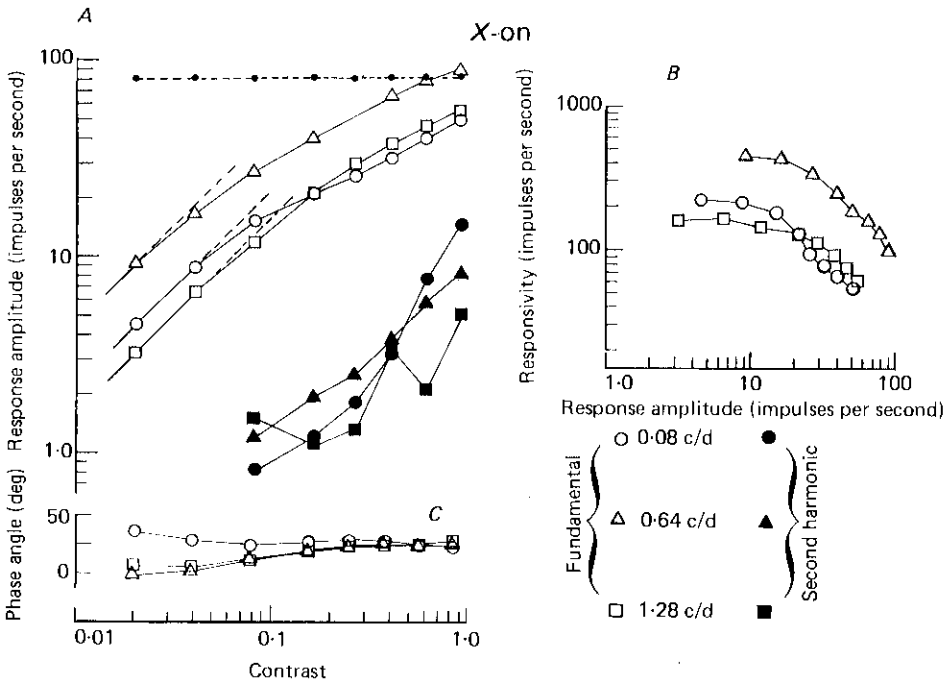

Fig. 2. Responses of an on-centre X cell (41/1) to drifting gratings (2 Hz) at three spatial frequencies and various contrasts. Open symbols refer to the fundamental, large filled symbols to the second harmonic. *A*, response amplitude *versus* contrast. The diagonal dashed lines represent proportionality of response with contrast. Small filled symbols and nearly horizontal dashed line show the mean firing rate whose range for all three spatial frequencies was 78–84 impulses per second. *B*, responsivity *versus* response amplitude at which responsivity was measured. *C*, phase angle of the fundamental response component *versus* contrast.

In their original description Enroth-Cugell & Robson (1966) claimed no more than that X cells showed linear spatial summation for contrast stimuli, that is that the magnitude of the responses to such stimuli depended on the resultant of a weighted linear summation (over the spatial extent of the receptive field) of signals proportional to the local contrast. In fact it appears (Victor & Shapley, 1979) that X cells may behave linearly in a somewhat stronger sense and within certain limitations generate responses linearly related to the resultant of such a linear spatial summation.

Response at different contrast levels

In a linear mechanism the response to a sinusoidal input will be a sinusoid of the same frequency. Thus, if the X cell is linear, we should find that response to a drifting

or sinusoidally contrast-modulated grating is accompanied by little change in the mean discharge rate and little response at the second harmonic frequency, while the amplitude of the fundamental component of the response should increase linearly with contrast and the phase remain constant. Fig. 2 shows measurements of the response of an on-centre X cell to drifting gratings of three spatial frequencies and various contrasts. The gratings drifted at that velocity required to modulate the local contrast at each point at 2 Hz. The open symbols in Fig. 2*A* show the fundamental amplitude as a function of contrast. In these log–log co-ordinates, linearity is indicated by a slope of one. At all three spatial frequencies the curves do not deviate markedly from straight lines with slopes of unity (dashed lines in Fig. 2*A*) at the lower contrasts although they all clearly fall below these lines when the response amplitude is more than 10–15 impulses per second.

In Fig. 2*B* the same measurements of response amplitude as are shown in Fig. 2*A* have been normalized with respect to the contrast of the stimulus and replotted against the amplitude of the response. This normalized response measure (amplitude of response in impulses per second divided by the contrast) will be referred to as the cell's *responsivity*. As would be expected from the discussion of the results already given, the cell's *responsivity* declines when the response amplitude is greater than 10–15 impulses per sec but appears to approach a constant value at lower levels of response.

Although the term *responsivity* has been introduced here simply as the normalized amplitude of a cell's response we shall later use it as a complex quantity to encompass both the phase as well as the magnitude of the response.

While the results of Fig. 2*A* and *B* appear to be typical of retinal X cells responding to stimuli whose spatio-temporal characteristics are not too far from optimum, we have been unable (because of the variability in the measurements introduced by the irregularity of ganglion cell discharges) to ascertain whether the range of amplitude linearity extends to the same response levels with less optimal stimuli. It might be expected that with such stimuli the behaviour would become non-linear at high contrast levels even when the response is small, but special experiments will be necessary to examine this satisfactorily. We have also found it impossible to decide how best to formulate the relation between fundamental response amplitude and contrast at high contrast levels where proportionality clearly breaks down. In many instances the experimental results can be fitted equally well by assuming that response amplitude increases at high levels with the square root of the contrast (Enroth-Cugell & Robson, 1966) as by assuming a logarithmic relation (Robson, 1975).

A further indication of the linearity of operation of a typical X cell is given by the horizontal dashed line in Fig. 2*A* which shows that, as would be expected for a linear device, the average discharge rate is unaffected by contrast, though it can also be seen that, contrary to the linear prediction, the X cell does produce some second harmonic response (filled symbols). However, relative to the fundamental, this component is small. In the range of contrast that we ordinarily used the second harmonic amplitude was typically no more than one-tenth that of the fundamental. The phase of the fundamental response as a function of contrast is shown in Fig. 2*C*. While the data depart systematically from the complete independence of phase and contrast required by linearity, the effects are small.

Response as a function of spatial phase

Yet another indication of the linearity of the behaviour of X cells is provided by examining how the amplitude of the response to a contrast-modulated grating pattern varies with the spatial phase of the pattern relative to the middle of the cell's receptive field. Fig. 3*A* and *B* shows such measurements for a typical X cell at two spatial frequencies, one approximately optimum for the cell (Fig. 3*A*) and one

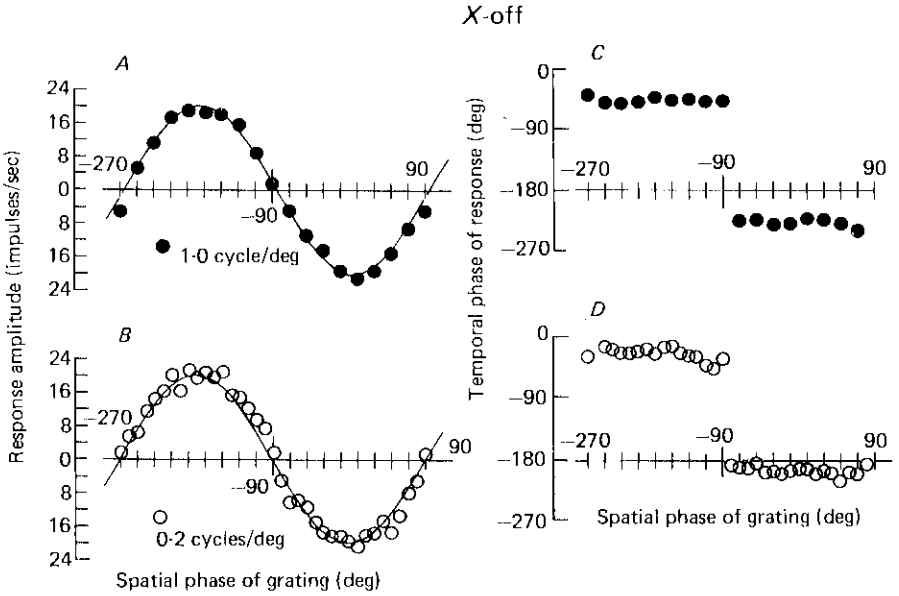

Fig. 3. Response as a function of spatial phase of the grating pattern for an off-centre X cell (37/16) at two different spatial frequencies (temporal frequency 4 Hz). Horizontal axis indicates the spatial phase of the stimulus. *A* and *B*, amplitude of the fundamental response component at contrasts of 0·05 and 0·1 respectively. In *A* and *B* the response amplitudes have been plotted above or below the zero axis according to whether the responses had phases approximately zero or −180°. This has been done to make clearer the sinusoidal form of variation of response amplitude with spatial phase. *C* and *D* are the corresponding temporal phases of the fundamental.

substantially lower (Fig. 3*B*). As first noted by Hochstein & Shapley (1976), a cell behaving linearly should show a response amplitude that is a sinusoidal function of the spatial phase of the grating. The examples of Fig. 3 are typical of how well this expectation is fulfilled by retinal X cells. We may also note as typical the abrupt 180° change in temporal phase of the response for spatial phases on either side of −90°, the position of null response for the grating (Fig. 3*C* and *D*).

Linearity of X cells

Taken all together, the findings reported above, which we believe to be quite typical of both on- and off-centre X cells (at least those within 10° of the area centralis), suggest that it would be wrong to suppose that these cells behave in an entirely linear manner even for stimuli at one mean luminance. However, it does not seem

unreasonable to expect that, so long as we restrict our attention to the behaviour of these cells in conditions in which these responses are not more than 10–15 impulses per second in amplitude, this behaviour can be quite generally described by a linear spatio-temporal transfer function. In collecting the data to be used in modelling X cells in this way we have therefore always chosen, as a result of preliminary trials, stimulus contrast levels which would produce response amplitudes as near 10 impulses per second as practicable. The results of these measurements are all normalized according to the actual contrast used and expressed as *responsivities*.

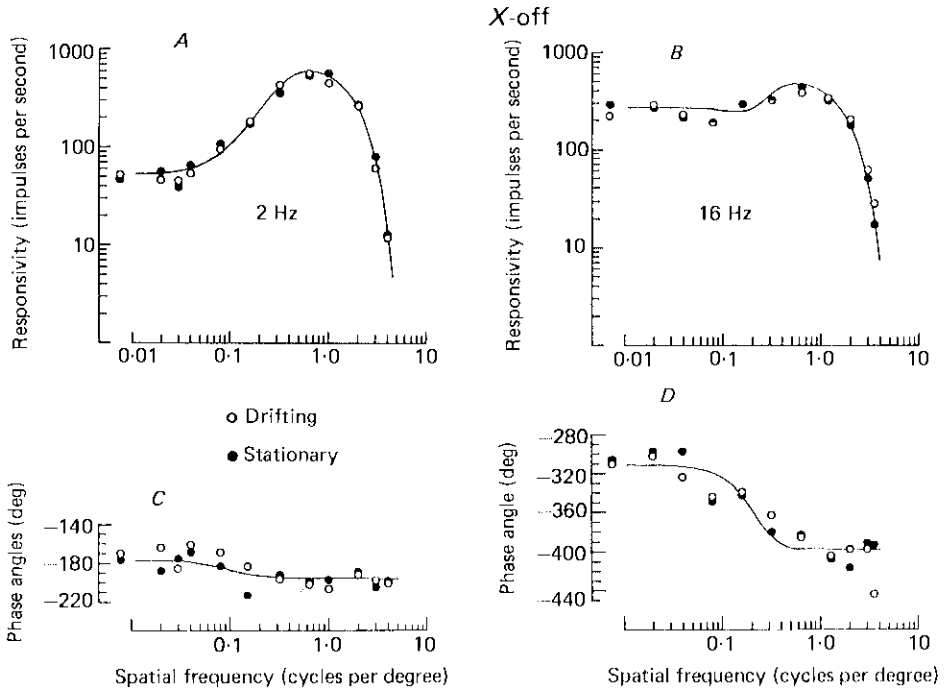

Fig. 4. Responses of an off-centre X cell (37/16) to drifting (○) and stationary (●) gratings. *A*, responsivities at 2 Hz as a function of spatial frequency. *B*, responsivities at 16 Hz. *C* and *D*, temporal phase of the responses at 2 and 16 Hz respectively. The curves are the best fit of the basic Gaussian centre–surround model with an additional surround delay and all six parameters adjusted at each temporal frequency to give the best fit (see text p. 294). In this and all following Figures of spatial contrast responsivity and phase functions the leftmost experimental points refer to zero spatial frequency, i.e. a temporally-modulated spatially-uniform field.

Drifting and stationary gratings

While Enroth-Cugell & Robson (1966) and most subsequent workers have used moving gratings of different spatial frequencies for studying the spatial characteristics of retinal ganglion cells and other visual neurones, there are advantages to be gained when the temporal aspects of a cell's behaviour are of interest, in using stationary patterns whose contrast is modulated in time. In particular, it is difficult to be certain with drifting gratings whether a temporal phase difference between stimulus and

response is not partly due to the existence of a spatial phase difference between the effective mid point of the receptive field and the zero phase position of the stimulus pattern (Lee, Elepfandt & Virsu, 1981).

Since we wished to obtain good measurements of the temporal phase of the responses of X cells we chose to use contrast-modulated stationary gratings rather than moving ones. We first, however, felt it desirable to check that concordant measurements could be obtained with both kinds of stimuli. In fact, in so far as X cells behave linearly, they should give the same response to a drifting grating as to a stationary grating of the same spatial frequency whose contrast is sinusoidally modulated at the same temporal frequency and whose spatial phase is 0° (i.e. a grating pattern with an anti-node centred on the cell's receptive field).

Fig. 4 shows how well this expectation is borne out for a typical X cell at two different temporal frequencies. In no X cell that we examined did we find any significant differences in either the responsivity or phase of the response with the two kinds of stimulus. Equally, while results for one direction of motion only are shown in Fig. 4, we found no evidence in this, or any X cell, of direction selectivity, a form of non-linearity not necessarily made evident by any other test.

Spatial frequency response functions

The spatial frequency responsivity and phase functions of X cells are well exemplified by the measurements shown in Fig. 4 (for an off-centre cell), in Figs. 5*A* and *B* (for an on-centre cell and another off-centre cell) and also in Fig. 9 (for three other cells). Typical features of X cell responsivity curves at all temporal frequencies up to 32 Hz are the existence of a maximum at some intermediate spatial frequency, a rapid decline towards zero at higher spatial frequencies and a less rapid decline at lower spatial frequencies to some asymptotic level. Note that the leftmost symbol in each data set in Figs. 4 and 5 corresponds to a spatial frequency of zero (i.e. it relates to the response of the cell to a uniform field whose luminance is sinusoidally modulated in time). Measurements of responsivity made at very low temporal frequencies (e.g. the 0·4 Hz data of Fig. 5*A*) show the typical band-pass form but are altogether lower, while measurements at temporal frequencies above a few Hz (e.g the 16 Hz data of Fig. 4 and the 8 and 16 Hz data of Fig. 5*B*) characteristically show a relatively small decline as the spatial frequency is reduced from the optimum to zero. Although the total extent of the fall in responsivity between that at the optimum and that at zero spatial frequency becomes fairly small when the temporal frequency is high (e.g. the 16 Hz data in Figs. 4 and 5), it does not usually disappear entirely at frequencies at least up to 32 Hz (the highest frequency routinely used). At the higher temporal frequencies (e.g. 16 and 32 Hz) the general level of responsivity at all spatial frequencies may decline while at frequencies significantly greater than 32 Hz the whole form of the curves may become rather different (see later and Fig. 12).

The characteristic way in which the temporal phase difference between stimulus and response in X cells depends upon the spatial frequency of the stimulus pattern and the temporal frequency at which its contrast is modulated is also clearly seen in Figs. 4, 5 and 9. At *temporal frequencies* around 2 Hz the response of an on-centre cell to a contrast-modulated grating of relatively high *spatial frequency* (e.g. Figs. 5*A*

and 9*C*) is usually approximately in phase with the stimulus. In other words the discharge rate rises and falls as the luminance at the middle of the receptive field increases and decreases. For off-centre cells the response is in the opposite sense: the phase difference is around −180°. For all cells, the response becomes relatively more delayed with respect to the stimulus as the temporal frequency is raised (phase difference becomes more negative) while as the temporal frequency is reduced below

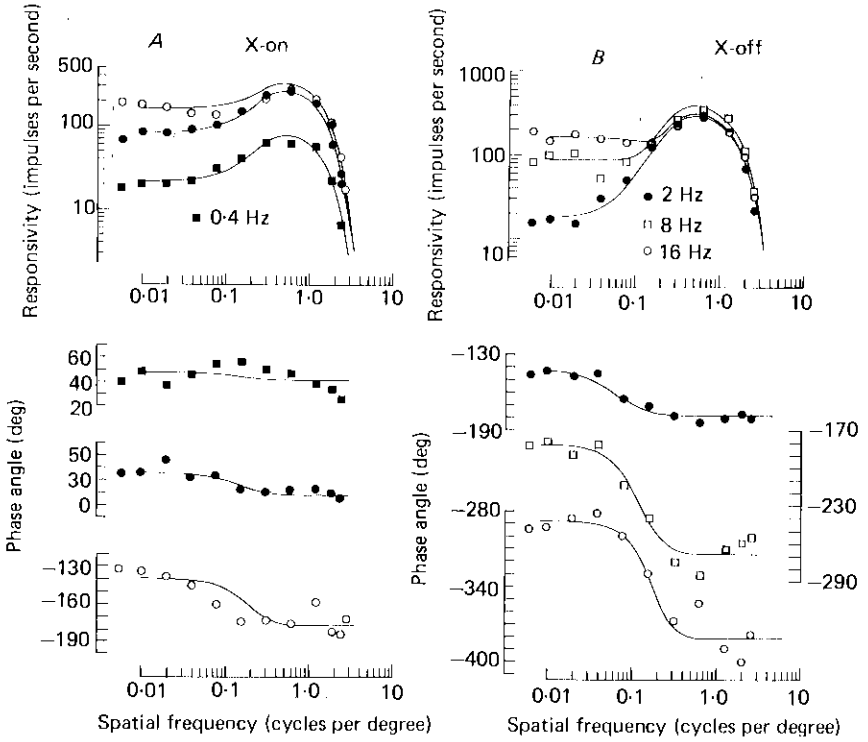

Fig. 5. Responsivity and temporal phase functions for *A*, an on-centre (27/7) and *B*, an off-centre (28/9) X cell. The curves are model predictions arrived at in the same way as in Fig. 4.

2 Hz the response becomes less delayed and may lead the stimulus by up to about 40° at frequencies of 0·2–0·5 Hz. For off-centre cells this means that at these frequencies the phase difference may become up to 40° less negative than −180° (i.e. it will lie between −180° and −140°). While the way in which stimulus–response phase difference depends upon temporal frequency is of considerable interest of itself, we shall not describe it in any more detail here as we are not intending in this paper to provide a complete model of the temporal aspects of X-cell behaviour. Rather we shall concentrate on another aspect of the phase measurements which relates more directly to the spatio-temporal interactions evident in X cell behaviour. This is the dependence upon *spatial* frequency of the *temporal* phase difference between the stimulus and the response. Typically the temporal phase difference appears to change from one constant value at high spatial frequencies to another (usually more positive) value at lower spatial frequencies. This change always occurs over roughly the range

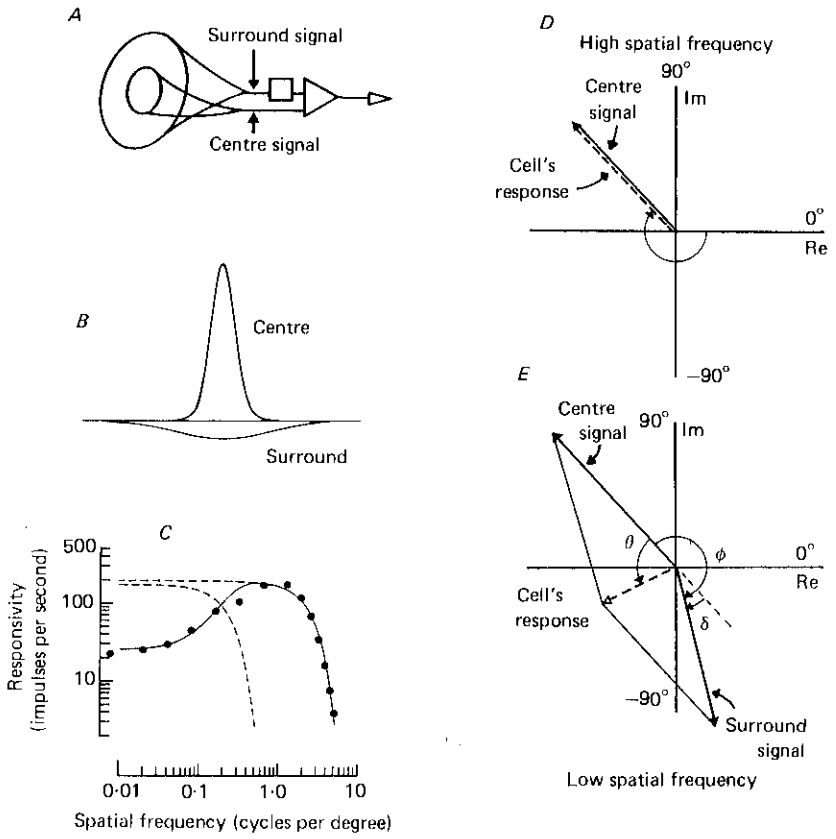

Fig. 6. *A*, diagrammatic representation of signal summation over a centre-surround organized receptive field. *B*, the radially Gaussian spatial weighting functions of the centre and the surround. *C*, the points are the experimentally determined (2 Hz) contrast responsivity of an on-centre X cell (31/17). The continuous line fitted to the data is the model's prediction of the cell's responsivity while the dashed lines represent the predicted contrast responsivity of centre and the surround (centre and surround strength, see p. 292). *D* and *E*, an explanation of the dependence of the phase of the cell's response upon spatial frequency for an off-centre cell. The diagram in *D* plots as phasors the centre signal and the cell's response; the diagram in *E* plots the centre and surround signals and the response of the cell. At a high spatial frequency (*D*) the cell's response is due exclusively to the centre mechanism, so the phase of the cell's response and the centre signal are equal while at a low spatial frequency (*E*) the surround produces a substantial signal which lags in phase behind that of the centre by more than 180 deg (angle ϕ). The resultant response of the cell leads that of the centre (by angle θ). For an on-centre cell all the phasors would be rotated by 180 deg.

of spatial frequencies between that at which the cell is maximally responsive and that lower spatial frequency at which the responsivity reaches its asymptotic level. The change in phase difference with spatial frequency is usually evident at all temporal frequencies although the magnitude of the change is usually greater at higher temporal frequencies and may disappear (or even be reversed) at the lowest frequencies (e.g. the measurements at the lowest temporal frequencies in Fig. 5*A* and 9*A* and *B*).

Modelling the X-cell receptive field

The responsivity of an X cell to grating stimuli is clearly dependent upon both the spatial and temporal frequencies at which it is measured. Moreover it is also clear that these two variables do not act independently in that the effect of changing temporal frequency is to change the shape of the spatial frequency responsivity function while the effect of changing spatial frequency is to change both the temporal phase of the response at any constant temporal frequency and also the way in which responsivity depends upon temporal frequency. This interdependence of spatial and temporal variables implies that the model proposed by Enroth-Cugell & Robson (1966) to account for the spatial frequency characteristics of X cells at 1 and 4 Hz cannot be correct. This model assumes the ganglion cell receptive field to be composed of separate antagonistic centre and surround regions (Fig. 6*A*) served by separate centre and surround mechanisms. Rodieck (1965) and Enroth-Cugell & Robson (1966) have represented the spatial weighting functions of centre and surround as concentric, radially symmetric Gaussian functions. The centre Gaussian is tall and narrow, the surround Gaussian is shallow, wide, and of opposite sign (Fig. 6*B*). Transformed into the spatial frequency domain the contrast responsivity function of the centre mechanism will extend to high spatial frequencies, that of the surround less far (Fig. 6*C*). In the context of the Gaussian centre–surround model, responses at high spatial frequencies may be attributed to the centre mechanism, those at low spatial frequencies to the combined actions of centre and surround (Fig. 6*C*). It is implicit in this model that the signals from centre and surround mechanisms reaching the ganglion cell are of opposite sign so that at low spatial frequencies, where both are of significant magnitude, their sum is less than that of the centre alone. In this way the ganglion cell responds less strongly at low spatial frequencies than at some higher spatial frequencies at which the surround signal has become relatively insignificant.

While this model does not explicitly include any time-dependent elements it is inevitable that the ganglion cell will reflect directly the time-dependent behaviour of those elements (e.g. the photoreceptors) common to both centre and surround pathways. While the temporal characteristics of such common elements probably contribute substantially to the observed dependence of response amplitude and phase on temporal frequency they cannot, of course, explain either the dependence of the temporal phase of the response upon spatial frequency (at a constant temporal frequency) or the differences in form of the spatial frequency responsivity function at different temporal frequencies.

Assuming that we wish to retain the basic Gaussian centre–surround model we may consider what modifications could be made to enable it to encompass our present findings. A simple modification which might be able to account for the dependence of response phase on spatial frequency would be the introduction of some differential delay into the centre and surround pathways. A qualitative argument (to be given below) as well as previous neurophysiological evidence (e.g. Rodieck & Stone, 1965) makes it seem reasonable to suppose that this may take the form of a phase delay in the surround pathway.

On this basis, the phase characteristics of the off-centre cells in Figs. 4*A* and 5*B* may be interpreted as sketched in Fig. 6*D* and *E*. At a high spatial frequency (and

low temporal frequency) at which the surround mechanism gives a negligible response the ganglion cell's response is equal to that of the centre mechanism, as shown by the phasors in Fig. 6*D*. As the spatial frequency is reduced the temporal phase of the centre signal will not change though its amplitude will increase slightly as shown in Fig. 6*E*. But at this low spatial frequency the surround mechanism produces a substantial signal at the ganglion cell which we suppose to lag in phase behind that of the centre signal by somewhat more than 180° (angle ϕ). The amount by which the surround lags the centre signal in excess of 180° (angle δ) is the *surround–centre phase delay*. The response of the cell which is equal to the sum of the two phasors now shows a phase *lead* (angle θ) relative to the centre signal. Thus as spatial frequency is reduced (and the length of the surround phasor increases) the ganglion cell's response phase should advance, as it is seen to do at all except the very lowest temporal frequencies in the results of Figs. 4, 5 and 9.

While the introduction of a phase delay into the surround pathway may account for the variation in temporal phase with spatial frequency it does not immediately do anything to explain why the form of the spatial frequency responsivity function changes with temporal frequency. To accommodate this effect we must suppose that one or more parameters of the model change with temporal frequency. While it is inherently likely that the phase lag introducted by any element providing a delay would increase with increasing frequency and while it is possible that this would produce an effect on spatial frequency responsivity of the observed kind, we cannot be at all certain of this without quantitative comparison of model predictions and experimental results.

An X-cell model with differential centre–surround phase delay. We can represent the responsivities of the centre and surround mechanisms of the ganglion cell stimulated by a grating of spatial frequency u by the complex numbers $R_c(u)$ and $R_s(u)$ respectively. If the signal from the surround mechanism passes to the summing point via a device (Fig. 6*A*) whose effect on the signal can be represented by a complex gain G_d then the spatial frequency responsivity function of the ganglion cell $R_g(u)$ is given by

$$R_g(u) = R_c(u) + G_d R_s(u) \tag{4}$$

If the centre and surround mechanisms have circularly symmetric Gaussian weighting functions of radius ρ_c and ρ_s then

$$|R_c(u)| = S_c \, e^{-(\pi \rho_c u)^2}, \tag{5}$$

and

$$|R_s(u)| = S_s \, e^{-(\pi \rho_s u)^2}, \tag{6}$$

where S_c and S_s are the *strengths* of the centre and surround at a given temporal frequency. The *strength* of a receptive field mechanism may be thought of as the responsivity that the ganglion cell would have if only that mechanism were connected to the cell and measurements were made with a stimulus of zero spatial frequency (the responsivity measured with a spatially uniform field).

We assume that at a given temporal frequency the signals from both centre and

surround mechanisms have been shifted in time with respect to the stimulus by the same phase angle P_c as a result of the action of components which are either common to both pathways or have identical effects.

Thus

$$\angle R_c(u) = \angle R_s(u) = P_c. \tag{7}$$

While Enroth-Cugell & Robson (1966) assumed that the device in the surround pathway only inverted the surround signal we now assume that it also changes the phase of the signal by the angle P_d. Thus

$$|G_d| = -1, \tag{8}$$

and

$$\angle G_d = P_d, \tag{9}$$

(if the surround signal is delayed by the device in the surround pathway P_d will be negative).

We now combine eqns. (4)–(9) to give the magnitude and phase of the spatial frequency responsivity function of the ganglion cell

$$|R_g(u)| = \{(S_c\, e^{-(\pi\rho_c u)^2})^2 + (S_s\, e^{-(\pi\rho_s u)^2})^2 - 2S_s S_c\, e^{-(\pi u)^2(\rho_c^2+\rho_s^2)} \cos(P_d)\}^{\frac{1}{2}}, \tag{10}$$

$$\angle R_g(u) = P_c + \tan^{-1}\frac{S_s\, e^{-(\pi\rho_s u)^2}\sin(P_d)}{S_c\, e^{-(\pi\rho_c u)^2} + S_s\, e^{-(\pi\rho_s u)^2}\cos(P_d)}. \tag{11}$$

We may note that eqns. (10) and (11) together contain six parameters, S_c, S_s, ρ_c, ρ_s, P_c and P_d, any of which may change with temporal frequency.

Validation of the model

We first consider whether eqns. (10) and (11) give an acceptable description of the way in which the magnitude and phase of the responsivity at a given temporal frequency varies with spatial frequency. In assessing the acceptability of our model we shall compare the predictions of a model having optimally adjusted parameters with the experimental results. We start by allowing all six parameters in eqns. (10) and (11) to be adjusted at each temporal frequency. The choice of the parameter values is made by adjusting them iteratively to minimize the difference between the predicted and measured complex responsivities at different spatial frequencies. We have chosen to find maximum likelihood estimates of the parameters which requires us to take into account the variability of the experimental measurements.

Response variability. Our measurements of ganglion cell responsivity are based on experimental determinations of the amplitudes of cosine and sine components of the discharge rate of the cell at the fundamental frequency of the stimulus. In preliminary studies we have found by making repeated measurements that the amplitudes of the sine and cosine components of the fundamental response appear to be independently normally distributed with equal variance. Moreover it seems that the variances of these orthogonal distributions are not only independent of each other but also to a great extent of the contrast of the stimulus and hence of the magnitude of the

response. In other words it seems that the response itself has little associated variability and the variability of the response measurements can mostly be ascribed to the intrinsic irregularity of the ganglion cell discharge.

In agreement with Derrington & Lennie (1982) we find that the spectral density of the on-centre X-cell discharge is roughly flat at low temporal frequencies but rises somewhat at frequencies approaching the mean firing rate. The spectral density of the discharge of off-centre X cells seems to be much the same as that of on-centre cells even though the mean discharge rate is rather less. Possibly because of their lower mean discharge rate the spectral density of off-centre cells may in fact rise at somewhat lower frequencies than in on-centre cells but the difference is not great.

While the variability of X cell discharges cannot be said to be fully characterized we feel justified in assuming here that the standard deviation of measured sine and cosine response component amplitudes in a given cell is constant. This means that experimental responsivity values which have all been derived from measurements in which the response magnitude is about the same (10–15 impulses per second) will have standard deviations proportional to the responsivity magnitude. The standard deviation of measured responsivity magnitudes derived from 10 sec runs is typically about 15%.

Estimation of parameters. Computation of maximum likelihood estimates of model parameters was performed using STEPIT, an optimization routine developed by Chandler (1965). This minimized the sum of the squared distances between predicted and measured responsivities where these distances were weighted inversely as the estimated standard deviation of the measurement (calculated assuming a standard deviation proportional to responsivity). Since measured response phasors had been found to be distributed independently in the principal directions in the phase plane, the distances between measured and predicted responsivities were computed in this plane.

The curves drawn in Figs. 4 and 5 have all been generated by the basic Gaussian centre–surround model with differential centre–surround phase delay (eqns. (10) and (11)). The values of all six parameters of the model have been adjusted at each temporal frequency to give the best fit. In comparing the curves with the experimental points it should be borne in mind that while the model used has six degrees of freedom, the same set of parameters has been used to generate both the magnitude *and* the phase curves at each temporal frequency. The experimental data set being fitted consists, in most cases, of eleven *pairs* of points having twenty-two degrees of freedom. It should also be noted that the phase scale is relatively expanded compared with the magnitude scale in the sense that the standard deviation of the magnitude measurements (about 15%) corresponds to a smaller vertical distance than the standard deviation of the phase measurements (about 9°).

It was clear from an examination of the more than eighty pairs of curves that had been generated to fit data from thirty-seven cells (those in Figs. 4 and 5 are typical examples) that in most cases the basic model could provide a satisfactory description of the observed behaviour at any one temporal frequency. This was borne out by a statistical analysis which, although imperfect, showed that only a small fraction of the model fits could be rejected on the grounds that the deviations of the experimental points were outside chance levels. Some of the experimental data sets

did show what appeared to be systematic deviations from the best fitting model curves especially at the extremes of temporal frequency (0·5 and 32 Hz). However we could discern no very obvious general pattern in these discrepancies. We conclude that at least in the range 1–16 Hz the X cell receptive field can be satisfactorily represented by a Gaussian centre–surround model with some differential centre-

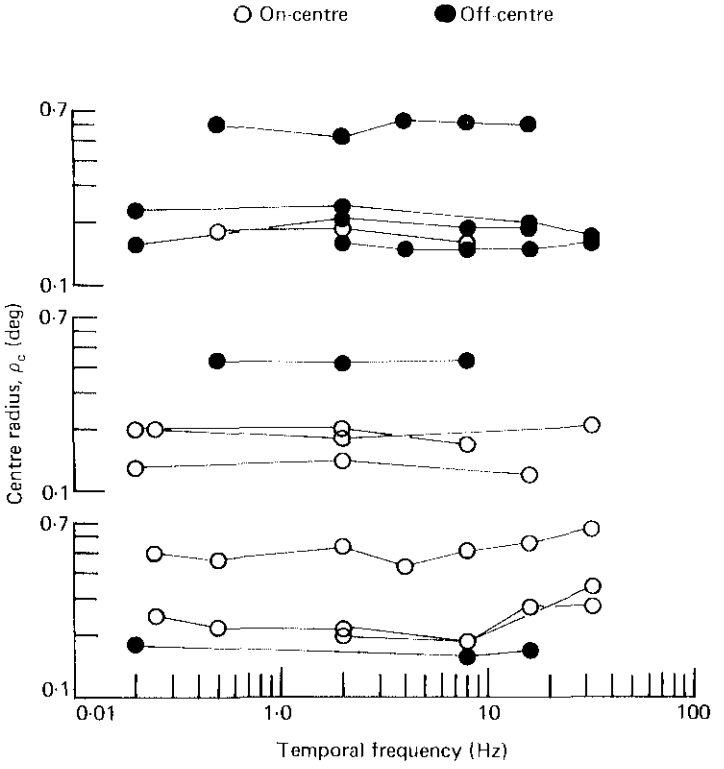

Fig. 7. Centre radius as a function of temporal frequency for eleven cells. Connected points are from the same cell. Estimates of radius were derived from best fits of the basic Gaussian centre–surround model with an additional surround delay (see p. 294). The separation into three groups is for convenience.

surround delay. It should be noted that some of the measurements at very low temporal frequencies (0·5 and 0·2 Hz) suggested that rather than the surround signal being *delayed* relative to the centre signal it might be slightly *advanced* (e.g. the 0·5 Hz phase *data* in Fig. 9). However this effect was always extremely small and never clearly out of the noise level of our measurements.

Temporal frequency dependence

We are now in a position to see how to explain the temporal frequency dependence of the spatial frequency responsivity functions by examining how the parameters of the best fitting model changed with changing temporal frequency. Fig. 7 shows for those X cells from which satisfactory measurements were obtained at three or more temporal frequencies, the radius of the receptive field centre of the best fitting

six-parameter model. It can be seen that while there was some variation in the centre radius at different temporal frequencies, there was no clear systematic variation common to all cells. Similarly, although there was greater variability in the best estimates of surround radius, again no clear trend was seen. We have therefore assumed that these parameters, centre and surround radii, can be considered to be constants independent of temporal frequency over the range we have studied.

After making this assumption the experimental data from which the estimates of Fig. 7 were derived were re-analysed. In this re-analysis a more constrained version of the basic model incorporating the assumption of constant radii was fitted to the data. While at each temporal frequency the four strength and phase parameters (S_c, S_s, P_c and P_d) were all allowed to vary freely, the same size parameters (ρ_c and ρ_s) were used at all temporal frequencies. All the experimental data for one cell (at several temporal frequencies) were fitted simultaneously so that the final best estimates of centre and surround radii were based on measurements made at a number of different temporal frequencies. Fig. 8 shows results from this re-analysis.

Surround–centre strength ratio. The ratio of surround to centre strengths at different temporal frequencies is plotted for eleven X cells in Fig. 8*A*. It has been supposed that a reduction in this ratio with increasing temporal frequency might account for the observed changes with temporal frequency of spatial frequency contrast sensitivity curves in retinal ganglion cells (Derrington & Lennie, 1982) and in analogous psychophysical effects (e.g. Robson, 1966; Burbeck & Kelly, 1981). Fig. 8*A* suggests that rather than there being a reduction in this ratio at high temporal frequencies, the ratio may even increase slightly. It is probably more reasonable, however, to interpret the results in Fig. 8*A* as indicating that, over the range of temporal frequencies examined, there is no significant change in the ratio of surround to centre strengths.

To what then, can the change in responsivity with temporal frequency be ascribed?

Surround–centre phase delay. Fig. 8*B* shows for the same eleven X cells the best estimates of the surround–centre phase delay at different temporal frequencies derived from the same fits of the constant-radii model. Despite the variability of the estimates there is a clear trend, the surround–centre phase delay increasing with increasing temporal frequency. Such behaviour might be modelled in many ways but two simple possibilities may be considered. First, we might suppose the device in the surround pathway to have the characteristics of a *transport delay*, that is to delay the signal by a fixed time and have no effect upon the amplitude of the transmitted signal. The phase delay provided by such a device is proportional to temporal frequency.

A second simple possibility is that the device in the surround pathway might have the characteristics of a single-stage *low-pass filter*. Such a device produces a phase delay which increases with increasing temporal frequency to a maximum of 90° while it reduces the amplitude of the transmitted signal by an amount which also increases with increasing frequency.

To choose between these two possibilities the experimental results from the eleven X cells for which measurements had been made at three or more temporal frequencies were analysed yet again. This time it was assumed not only that the centre and surround radii were constants independent of temporal frequency and that the ratio

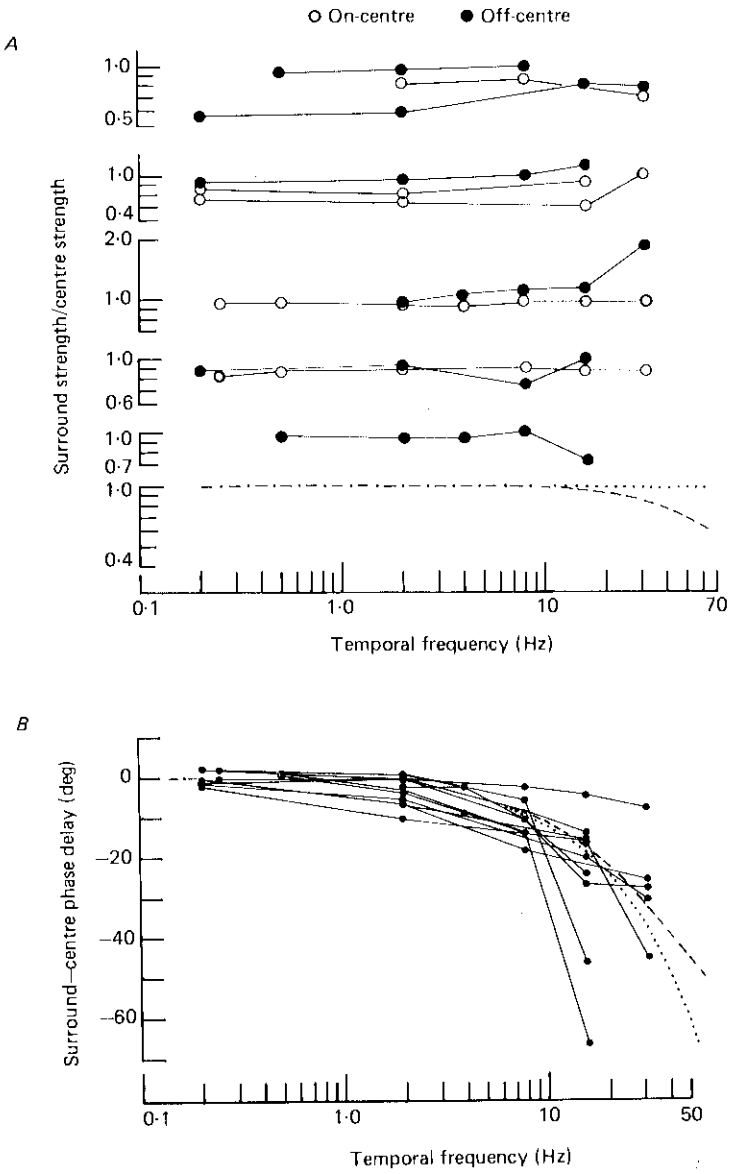

Fig. 8. *A*, ratio of surround to centre strength as a function of temporal frequency. Each set of connected points is from a single X cell. Strengths were estimated from the best fits of the model described in text (p. 296). The dashed curve at the bottom of *A* is the model's prediction of the surround–centre ratio when the surround–centre phase lag is assumed to be due to a single-stage low-pass filter with a time constant of 3·25 msec in the surround pathway. The dotted line in *A* is the model's prediction of the ratio assuming an additional 3·4 msec transport delay in the surround pathway. *B*, surround–centre phase lag as a function of temporal frequency. Connected points are from individual cells. Lags were estimated from the best fits of the model described in text. The dashed line is the model's prediction of the surround–centre phase lag assuming a single-stage low-pass filter with a time constant of 3·25 msec; the dotted line is the prediction based on a 3·4 msec transport delay in the surround pathway.

of surround to centre strength was constant, but also that the device in the surround pathway could be characterized either as a transport delay with fixed delay time or as a single-stage low-pass filter with a fixed time constant. This re-analysis provided best estimates of delay time or time constant for each cell. These estimates were quite varied (delay times lay between 1·2 and 7·7 msec and time constants between 0·9 and

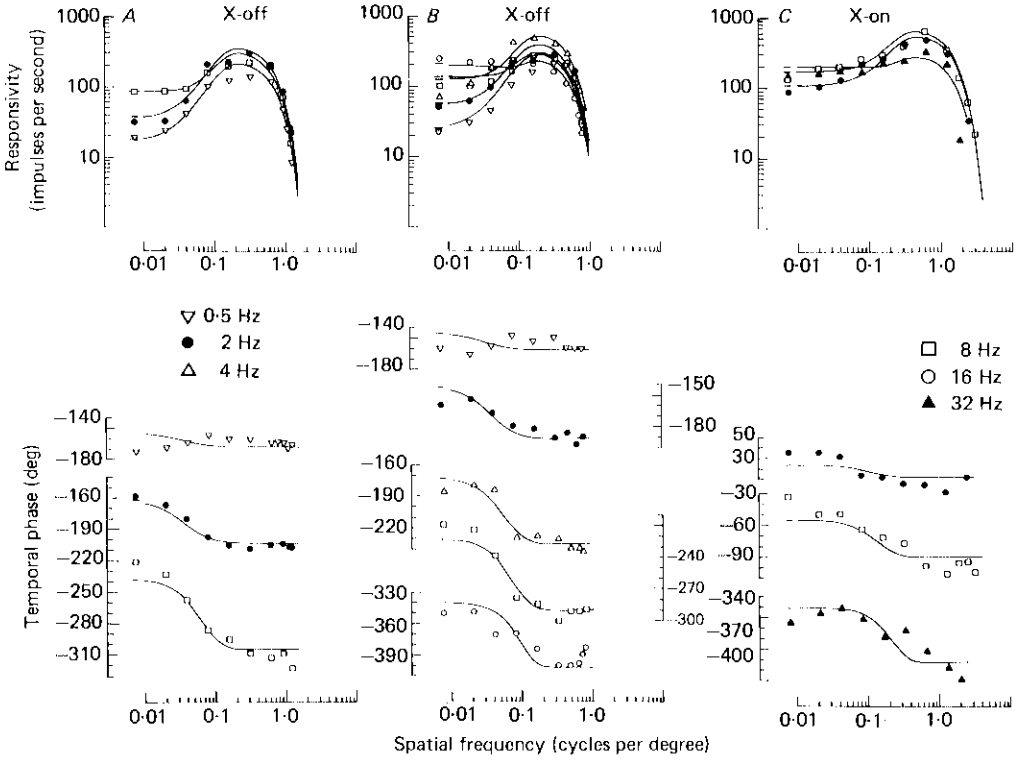

Fig. 9. Responsivity and phase functions for one on- and two off-centre X cells. Several temporal frequencies were used for each cell. The superimposed curves are the best fits of the Gaussian centre-surround model assuming a fixed time delay in the surround pathway (see below). *A*, cell 35/13; *B*, cell 35/16; *C*, cell 30/16.

7·1 msec) but had median values of 3·4 and 3·25 msec respectively. These median values have been used to compute the amplitude and phase characteristics plotted as dashed and dotted lines respectively in Fig. 8 *A* and *B*.

While the results shown in Fig. 8 *A* and *B* do not provide a very good basis for choosing between these two possibilities, it seemed that the predictions of the transport-delay might be slightly better than those of the low-pass filter model. This was confirmed by a statistical analysis which showed that the transport-delay model provided a slightly better fit in eight of the eleven cells while the low-pass-filter model provided a slightly better fit in two. The differences were not, however, large.

A Gaussian centre–surround model with transport delay. The results shown in Fig. 9 *A–C* for three X cells have been fitted by a model with Gaussian centre and surround weights in which the only time-dependent effect on centre–surround characteristics

is provided by a transport delay in the surround pathway. This model seems to provide a generally acceptable fit. We should note that for the cells in which results are shown for three temporal frequencies (Fig. 9*A* and *C*) the model has ten degrees of freedom while the data have sixty and fifty-eight respectively. In Fig. 9*B* the model has 14 and the data have 90 degrees of freedom.

While, as mentioned earlier in connection with Figs. 4 and 5, the measurements obtained on X cells at the extreme temporal frequencies (0·5 and 32 Hz) are less well described by a Gaussian model, the model with a transport delay in the surround pathway seems to provide a sufficiently good fit to be accepted as a useful description.

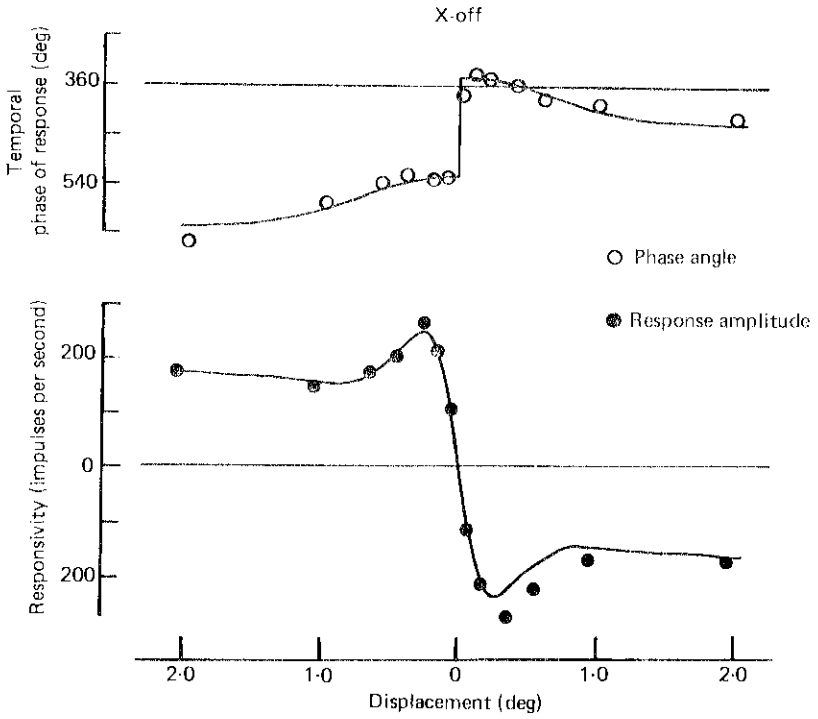

Fig. 10. Responsivity and temporal phase for an off-centre X cell (28/9) responding to an edge stimulus. Temporal frequency was 16 Hz. The curves are predictions from the best fit of the model (see p. 294) to the responses of the same cell as shown in Fig. 5*B*. For clarity responsivity is plotted below the zero line when the phase changes by 180°.

Response to a spatial edge

One value of a spatio-temporal model of the X cell is its ability to predict responses to arbitrary stimuli. For example, Enroth-Cugell & Robson (1966) were able to predict the amplitude of response to an edge from their model of the spatial receptive field. Here we show, as an example, that the present model is capable of predicting both amplitude and phase of the temporal response to a spatial edge. Fig. 10 shows magnitude and phase measurements for an edge displaced by various amounts from the receptive field centre. The contrast of the edge was varied sinusoidally in time at a frequency of 16 Hz. These data were collected from unit 28/9, whose spatial

frequency responsivity functions are shown in Fig. 5. A model (with the parameters adjusted to generate the curves in Fig. 5) has been used to predict responsivity as a function of edge position. These predictions are shown by the curves in Fig. 10. Considering that no further adjustments of the parameters were made the model is seen to provide a good prediction of the experimental measurements made with the edge.

Cells, other than X cells, with linear spatial summation

By recording directly from ganglion cells with an intraretinal electrode it is possible to record in quick succession from several different cells located close together. When we obtained recordings in this way from several X cells we invariably found that the cells' spatial characteristics, as shown by the shape of their spatial frequency responsivity functions, were very similar (even if on- and off-centre cells were considered together). On occasion however, we found a cell which might, by a test of linearity of spatial summation, have been classified as an X cell had it not had a strikingly more regular discharge, a longer conduction latency and a spatial frequency responsivity function displaced to distinctly lower spatial frequencies than that of adjacent X cells. Although we have only examined in any detail the behaviour of seven of these cells, all of which had an on-centre, we are convinced that they form a rather homogenous group and that they must be considered separate from the X cells proper. These cells will be referred to as Q cells.

The linearity of Q cells was manifest not only in (1) the way in which the amplitude of their response to a contrast-modulated sinusoidal grating varied as a sinusoidal function of the grating's spatial phase, but also (2) the relatively low amplitude of the second harmonic component in this response, even when the spatial frequency was above the optimum, (3) the absence of a change in the cell's mean firing rate induced by a periodic stimulus, (4) the proportionality of the amplitude of their response to stimulus contrast, and (5) the constancy of the temporal phase of the cells' response to stimuli of different contrasts. That is, in these respects the behaviour of Q cells was very much the same as that of X cells.

Similarly there was essentially no difference in the form of the responsivity or phase functions of Q cells and those of X cells except in so far as the former responded at lower spatial frequencies than X cells and as a rule had lower responsivities. (An example is shown in Fig. 11). Considering these similarities to X cells it is not surprising that the model we have found to fit the X cell data can provide as good a description of the behaviour of Q cells. This can be appreciated from the examples shown in Fig. 11 where the continuous curves are the best fits of a model with centre and surround radii independent of temporal frequency.

As would be expected from inspection of spatial frequency response functions for Q cells, the main consistent difference in the models fitted to these and X-cell data lies in the radii of the receptive field centres. The values of this parameter were larger than the center radii of X cells by a factor of two to three at all retinal eccentricities. Though we have as yet too little data to be certain, it seems possible that the additional surround delay in Q cells may also be substantially larger than in X cells.

We measured the antidromic latencies of all seven Q cells in response to stimulation of the optic nerve at the chiasm. The latencies ranged from 5·5 to 7·5 msec. These

values may be compared with those for the seventy-two X cells which we also measured. Of these only one (at 5·3 msec) was greater than 4·5 msec. We have examined the maintained discharge of five Q cells objectively. In the presence of an unmodulated uniform field (440 cd m^{-2}) the mean firing rate of these cells was slightly less than that of X cells. However, the coefficient of variation of the interspike interval distribution (standard deviation of the intervals divided by the mean interval) was only about one third that of X cells.

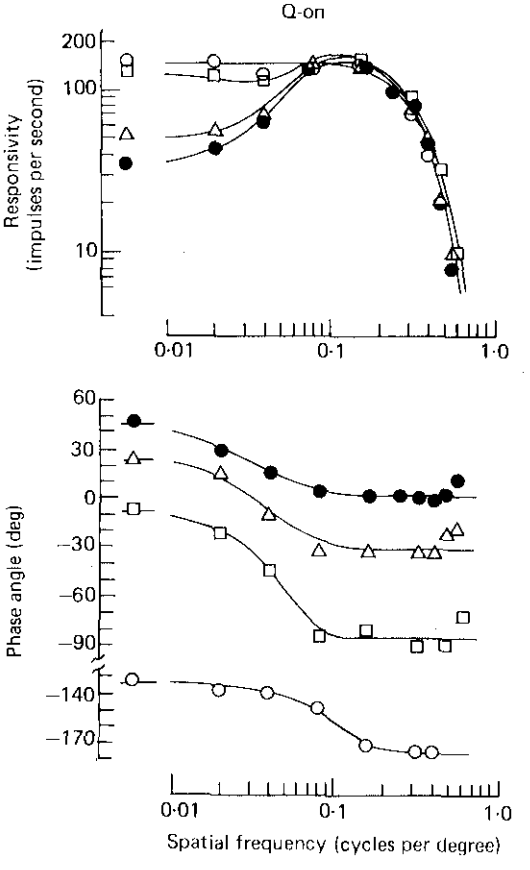

Fig. 11. Responsivity and temporal phase of an on-centre Q cell (35/22). The curves are the predictions of the centre–surround model assuming that centre and surround radii do not vary with temporal frequency (see text p. 296). The horizontal lines through the leftmost symbols in the phase plot represent the asymptotic level of the model's phase prediction.

It should be noted that we are not claiming to have discovered a new ganglion cell class in the cat retina for it is most likely that our Q cells constitute a sub-group within Stone & Fukuda's (1974) tonic W cells, or using Cleland & Levick's (1974) terminology, within the sluggish centre–surround class (c.f. Levick & Thibos, 1980). That we did not encounter any off-centre cells of a similar kind is probably because these have no maintained discharge at the high mean luminance used in our experiments (Cleland, B. G., personal communication).

Very high temporal frequencies

While the Gaussian centre–surround model of the receptive field responsivity function appears to provide a satisfactory fit to measurements of spatial frequency responsivity at temporal frequencies of 1–16 Hz it has already been noted that there is a tendency for the fits to become slightly worse at the highest temporal frequency

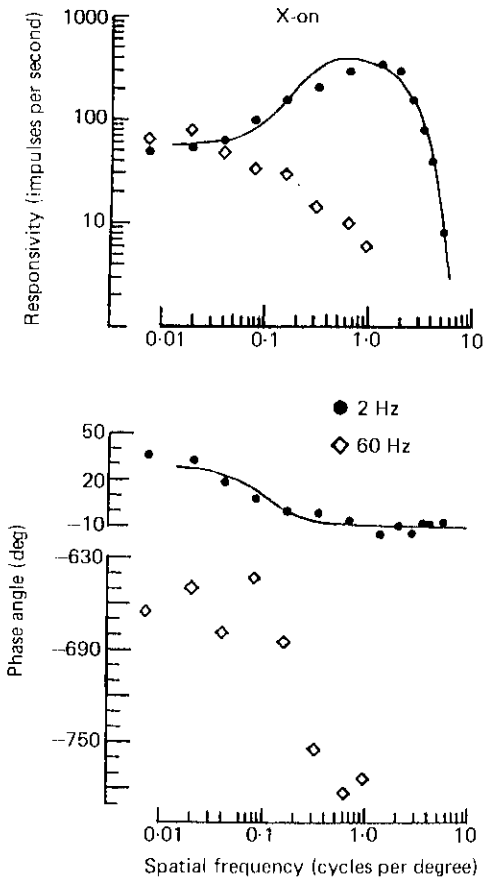

Fig. 12. Responsivity and temporal phase for an on-centre X cell (31/12) at 2 and 60 Hz. The curves drawn through the 2 Hz data are the best fit to the Gaussian centre–surround model.

at which we routinely made measurements (32 Hz). For a few X cells we made measurements at even higher frequencies. Fig. 12 shows an example of the typical spatial frequency response of a cell at 60 Hz, as well as at 2 Hz for comparison. Although our method of response measurement is not fully adequate at frequencies as high as 60 Hz this will not affect the two features of the response functions at this high frequency which are particularly significant. First, it is quite clear that the temporal phase of the response is as dependent upon spatial frequency as at low temporal frequencies. This could be taken as an indication that there are still two mechanisms with distinctly different spatial frequency responsivity functions

contributing to the over-all behaviour at very high frequency. However, the form of the responsivity function is quite unlike that at lower temporal frequencies, having its maximum at, or certainly very close to, zero spatial frequency and falling off steadily above 0·01 cycle per degree to become too small to be measured above 1·0 cycles per degree. A fit of the model containing spatial parameters derived from the 2 Hz data would give a very poor fit to the 60 Hz data. It may be possible to fit a Gaussian centre–surround model if we allow that centre and surround radii both change considerably at very high temporal frequencies. Alternatively one may speculate that at these very high temporal frequencies the centre contributes nothing to the cell's discharge (for which we have some indirect experimental evidence) and that the behaviour of the surround changes rather abruptly above 35–40 Hz. Support for a notion of this kind comes from the work of Foerster, van de Grind & Grüsser (1977*a*,*b*) who report that cat retinal horizontal cells appear to increase their summation areas rather dramatically above about 40 Hz.

DISCUSSION

The experimental work reported in this paper can be seen as an extension of that of Enroth-Cugell & Robson (1966), which showed how cat retinal ganglion cells can be characterized by measurements of their sensitivity to grating stimuli and how these measurements can be understood in terms of Rodieck's (1965) model of the ganglion cell receptive field. This earlier work, incidentally, made it clear that Rodieck's simple antagonistic centre–surround model with Gaussian spatial weighting in both centre and surround was only *generally* applicable to a subset of retinal ganglion cells, namely those cells which showed approximately linear spatial summation. Enroth-Cugell & Robson (1966) identified one class of such cells and called them X cells.

We have now examined further the responses of cat retinal X cells to grating stimuli, looking not only at the temporal phase of the responses as well as their amplitude but also at the effect of making measurements over a range of temporal frequencies. We have also looked at the behaviour of another class of ganglion cells which show linear spatial summation.

Linearity. In interpreting the results of these measurements it has been assumed that the linearly summating ganglion cells behave altogether linearly for stimuli which produce responses of relatively small amplitude. This has been tested directly in a number of ways using sinusoidally contrast-modulated or drifting gratings. These simple tests all indicate that a range of approximately linear operation does indeed exist. However it seems that the range is quite limited, being restricted to responses with amplitudes of no more than 10–15 impulses per sec. This limitation of the range of linear operation seems to be quite consistent with the results of Shapley & Victor's (1978) elegant study of the non-linearities of retinal ganglion cell behaviour. These authors make the point that non-linearity of X-cell operation becomes more obvious at low temporal frequencies (below 2 Hz). We have not directly tested the linearity of ganglion cells at very low temporal frequencies, but some of the discrepancies we observed in fitting models at very low frequencies may have derived from non-linear effects.

It should be noted that the measurements reported here, and indeed virtually all

reported measurements of ganglion cell response, are based on the notion that information is signalled in individual optic nerve fibres as a modulation of the discharge rate. Thus in experimental studies responses are measured either directly from post-stimulus time histograms or by some process, such as Fourier analysis of the impulse train, which can provide equivalent measurements. This kind of analysis has often been justified by supposing that the nervous system will usually have available an ensemble of similar signals which can be combined together before being low-pass filtered to provide a representation of an input common to the nerve cells from which the ensemble of signals originates. While it was believed that the occurence of impulses in different ganglion cells was uncorrelated and that the statistics of ganglion cell discharges were rather precisely correlated with the mean rate (both findings of a study by Gestri, Maffei & Petracchi in 1966) there was little reason to doubt that discharge rate in individual optic nerve fibres was the relevant variable. However, it is now clear that the discharges in X cells with overlapping receptive fields can be highly correlated (Mastronarde, 1983) and it is not yet certain that the statistics of discharges from linearly summating ganglion cells are all characterized by a single variable (Gestri *et al.* probably studied Y cells). Thus it cannot be ruled out that physiologically significant signals are transmitted either in some other variable than the discharge rate of impulse trains from individual linearly summating cells or in some variable derived from more than one train. In either case our characterization of ganglion cell behaviour would probably be of little physiological significance.

Spatial frequency responsivity functions. Most of the measurements made on linearly summating ganglion cells were used to construct spatial frequency responsivity functions (e.g. Figs. 4, 5 and 9). The magnitude functions measured in this study at an intermediate temporal frequency (mostly at 2 Hz) were very similar to the contrast sensitivity functions of X cells reported by Enroth-Cugell & Robson (1966) and to the sensitivity functions measured by Derrington & Lennie (1982) under similar conditions. As in these other studies there was considerable variation from cell to cell in the extent of the attenuation of responsivity at low spatial frequencies. However, a fair indication of the range of attenuations of X cells is given by Figs. 4, 5 and 9.

It is interesting to note that in several cells studied early in this work the magnitude of the responsivity at 2 Hz fell at a low spatial frequency very close to zero, only to rise again, at even lower spatial frequencies, toward the zero frequency asymptote. In these cells it appeared that the phase of the response more or less reversed as the spatial frequency was reduced from just above that giving the minimum response to one just below it. This behaviour is consistent with the strength of the receptive field surround in these cells being somewhat greater than that of the centre. In such a case it is to be expected that there would be some spatial frequency at which the signals from centre and surround would have the same amplitude and most nearly sum to zero. How nearly these signals would actually cancel would depend upon how nearly they were exactly 180° out of phase. It is not clear why this behaviour was not observed in later experiments, though Linsenmeier, Frishman, Jakiela & Enroth-Cugell (1982) have provided some evidence that the ratio of surround-to-centre strengths may depend upon anaesthetic level or type.

Measurement of the temporal phase of the response of ganglion cells to drifting grating stimuli appears to have been previously attempted only by Lee *et al.* (1981). They reported that while the temporal phase of the response to a drifting grating depended upon the spatial phase difference between the middle of a cell's receptive field and the zero phase reference point of the stimulus screen (as it must) there was no independent effect of spatial frequency upon the temporal phase of the response. It is not entirely clear why these authors did not observe the dependence of temporal phase upon spatial frequency that was a rather obvious feature of the present experiment. A contributing factor may be that Lee *et al.* made measurements at spatial frequencies only down to about 0·2 cycles per deg whereas in many cells the effect of reducing spatial frequency upon the temporal phase becomes obvious at spatial frequencies of 0·1 cycles per deg and less.

Both Lee *et al.* (1981) and Derrington & Lennie (1982) examined the effect of changing temporal frequency on the magnitude of the response of X cells to drifting gratings. While Derrington & Lennie observed much the same changes as we did (in particular the marked reduction of low spatial frequency attenuation which could occur at high temporal frequencies), Lee *et al.* concluded that there was usually little effect. Again it is difficult to account for the differences in Lee *et al.*'s experience but it appears that they mostly examined the amplitude of responses to gratings of quite high contrast, under which conditions the cell's behaviour may have been quite non-linear, rather than at contrasts low enough for the cells to be operating more or less linearly.

Receptive field shape. In modelling the X-cell receptive field we have adopted the formulation of Rodieck (1965) and Enroth-Cugell & Robson (1966) which assumes that the centre and surround regions are concentric and have radial symmetry. That the centre and surround regions of the ganglion cells we studied were concentric was indicated both by the null position of sinusoidal gratings being essentially independent of spatial frequency and the amplitude and phase of the responses to drifting gratings being unaltered by reversing the direction of motion. While these tests were not performed on every cell, no exceptions were seen. However, in so far as we tested very few cells with other than vertical gratings, we can really only be at all certain that centre and surround regions were not horizontally displaced.

Levick & Thibos (1982) have recently found that retinal ganglion cells may show a slight anisotropy when tested with drifting gratings at different orientations. We have not made measurements of this kind and so have no information about the degree of anisotropy that might have been shown by the particular cells we studied. While exact modelling of ganglion cells showing such anisotropy would necessitate formulation of the receptive field weighting functions in two dimensions coupled with extra experimental measurements, an incorrect assumption of radial symmetry will only result in slightly inexact estimates of the receptive field size parameters.

Modelling the spatial frequency response function. Models of spatial frequency sensitivity functions which can explain the effects of varying temporal frequency on the form of these curves have been proposed not only for retinal ganglion cells (Derrington & Lennie, 1982) but also in a psychophysical context (Burbeck & Kelly, 1980). In both cases only magnitude data were available and the models have not been required to predict a phase characteristic as well.

In both cases the authors have noted that while these sensitivity functions cannot be represented as the product of independent spatial and temporal functions (they are not *separable* in space and time), they can be represented as the sum of two spatio-temporal functions which are themselves each separable. These two spatio-temporal functions have been considered to relate either directly (by Derrington & Lennie, 1982) or reservedly and hypothetically (by Burbeck & Kelly, 1980) to centre and surround mechanisms of receptive fields. In both cases these authors have, while recognizing the significance of ignoring phase differences between centre and surround signals, settled for models which account for the changes in spatial frequency functions at different temporal frequencies by assuming that the relative strengths of centre and surround change with changing temporal frequency.

At least as explanations of ganglion cell behaviour such models are inadequate as they make no prediction of the effect of changing spatial frequency on the temporal phase of the response at a fixed temporal frequency. We have found it necessary to assume that there is differential phase delay between centre and surround signals to account for the phase behaviour at a fixed temporal frequency. Furthermore it is clear that it is a change in the surround-to-centre phase delay rather than change in the ratio of surround-to-centre strengths, which causes the differences in the shape of the spatial frequency responsivity function at different temporal frequencies.

Even though it may not be entirely appropriate to model the effect of changing temporal frequency on the surround–centre phase difference by assuming a transport delay in the surround pathway as we have proposed and Derrington & Lennie (1982) have considered, it still seems to us that it is less appropriate to assume that the ratio of surround-to-centre strengths changes in arbitrary manner with temporal frequency than that the phase difference changes arbitrarily while the strength ratio remains constant. At least with this latter assumption the phase behaviour at constant temporal frequency can be explained as well as the magnitude behaviour.

It would strengthen our proposal that temporal aspects of centre-surround interactions in ganglion cell receptive fields can be adequately understood in terms of the existence of an additional temporal delay in the surround pathway if any obvious anatomical basis for such a delay had been described. However, we know of no such basis. In the context it is worth noting that the magnitude of the delay required to explain our measurements was found to be rather small having a median value of only 3·4 msec (Derrington & Lennie, 1982, found 0–3·6 msec). This value is much less then that derived from experiments with flashing spots and annuli (e.g. Enroth-Cugell & Lennie, 1975) though it is not clear why.

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