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NONLINEAR SPATIAL SUMMATION AND THE CONTRAST GAIN CONTROL OF CAT RETINAL GANGLION CELLS

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SUMMARY

1. We studied how responses to visual stimuli at spatially separated locations were combined by cat retinal ganglion cells.

2. The temporal signal which modulated the stimuli was a sum of sinusoids. Fourier analysis of the ganglion cell impulse train yielded first order responses at the modulation frequencies, and second order responses at sums and differences of the input frequencies.

3. Spatial stimuli were spots in the centre and periphery of the cell's receptive field. Four conditions of stimulation were used: centre alone, periphery alone, centre and periphery in phase, centre and periphery out of phase.

4. The effective first order response of the centre was defined as the response due to centre stimulation in the presence of periphery stimulation, but independent of the relative phases of the two regions. Likewise, the effective first order response of the periphery was defined as the response due to periphery in the presence of centre stimulation, but independent of the relative phases of the two regions. These effective responses may be calculated by addition and subtraction of the measured responses to the combined stimuli.

5. There was a consistent difference between the first order frequency kernel of the effective centre and the first order kernel of the centre alone. The amplitudes of the effective centre responses were diminished at low frequencies of modulation compared to the isolated centre responses. Also, the phase of the effective centre's response to high frequencies was advanced. Such non-linear interaction occurred in all ganglion cells, X or Y, but the effects were larger in Y cells.

6. In addition to spatially uniform stimuli in the periphery, spatial grating patterns were also used. These peripheral gratings affected the first order kernel of the centre even though the peripheral gratings produced no first order responses by themselves.

7. The temporal properties of the non-linear interaction of centre and periphery were probed by modulation in the periphery with single sinusoids. The most effective temporal frequencies for producing non-linear summation were: (*a*) 4–15 Hz when all the visual stimuli were spatially uniform, (*b*) 2–8 Hz when spatial grating patterns were used in the periphery.

8. The characteristics of non-linear spatial summation observed in these experiments are explained by the properties of the contrast gain control mechanism which we have previously postulated.

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INTRODUCTION

Excitatory and inhibitory neural signals converge onto retinal ganglion cells from photoreceptors and interneurones which are sometimes a millimeter or more distant from the ganglion cell body. Indeed, the spatial summation performed by ganglion cells is one of the principal reasons why these cells are interesting to neurophysiologists. An investigator can manipulate the optical stimulus and thereby control the pattern of neural convergence. This makes possible a precise study of the mechanisms of neural integration in the retina.

In previous experiments we have studied indirectly the spatial summation performed by ganglion cells and proposed a new receptive field model. This model contains two new mechanisms: an ensemble of non-linear subunits which feed excitation into Y cells, and a contrast gain control which modifies the transfer characteristics of X and Y cells contingent on stimulus contrast (Hochstein & Shapley, 1976*b*; Victor, Shapley & Knight, 1977; Shapley & Victor, 1978). Both these mechanisms have a wide spatial extent; they overlap the conventional centre and surround mechanisms and extend far into the receptive field periphery.

In this paper we report direct measurements of the properties of spatial summation in cat retinal ganglion cells. Spatially distinct spots were modulated by sums of sinusoids. One of these spots filled the centre of the receptive field, and four other large spots were located in the periphery of the receptive field. There were systematic departures from simple linear summation. Analysis of the interaction between centre and periphery suggests that the contrast gain control (Shapley & Victor, 1978) is probably the dominant non-linearity. Furthermore, we suggest that the 'suppressive surround' found by others (Cleland & Levick, 1974; Jakiela, 1978 and personal communication) and the contrast gain control are probably identical mechanisms.

METHODS

Our methods for recording from the nerve fibres in the optic tract of the cat are described in detail elsewhere (Hochstein & Shapley, 1976*a*); we describe them briefly here.

We recorded extracellularly from optic tract fibres of adult cats anaesthetized with urethane and paralysed with a gallamine-alloferin mixture. For the duration of the experiments the e.c.g., e.e.g., blood pressure, core temperature, end-expiratory CO_2 and optics were monitored and maintained at physiological levels. Tungsten-in-glass micro-electrodes were lowered into the brain within a sealed chamber. The electrode position was adjusted until the extracellularly recorded action potentials of a single unit reliably triggered a discriminator circuit. The times of occurrence of the shaped pulses produced by the discriminator were recorded to within 0·1 msec by a PDP 11/20 computer.

The visual stimulator was a Hewlett-Packard 1321A cathode ray tube display. It was at a distance of 57 cm from the cat and had an area of 20 × 20 cm, which spanned a visual angle of 20° × 20°. The mean luminance of the display was 10–20 cd/m^2. Spatial patterns were produced on the cathode ray tube by a raster generated by specialized electronics (Shapley & Rossetto, 1976). The frame rate of the raster was 200 Hz, corresponding to the frequency of the sawtooth wave form on the X-axis input.

Categorization of optic tract fibres

The optic disks were mapped onto a tangent screen with an ophthalmoscope. Whenever the impulses of a single optic tract fibre were isolated, the midpoint of the receptive field was mapped on the tangent screen. The unit was classified as on-centre or off-centre. Then the fibre

was classed as an X or Y fibre by means of a modified null test (Enroth-Cugell & Robson, 1966; Hochstein & Shapley, 1976*a*). In this procedure contrast reversal gratings were used as spatio-temporal stimuli. The contrast used was in the range 0·2–0·4. Spatial frequency was increased until the unit's impulse train was barely synchronized to the temporal frequency of the contrast reversal. If the modulation of the fibre's discharge was at the modulation frequency, and if the amount of modulation depended on the spatial phase for such barely resolvable gratings, the cell was classed as an X cell. Y cells were those which gave spatial phase-insensitive responses to barely resolvable gratings; the responses in the Y cells were always dominated by the second harmonic of the stimulus modulation frequency (frequency doubling) when the spatial stimulus was a just-resolvable grating (Hochstein & Shapley, 1976*a*; Victor *et al.* 1977).

Visual stimuli for spatial summation experiments

The visual stimuli used in these spatial summation experiments consisted of two separate spatial patterns modulated independently in time, presented on a steady background. Each spatial pattern was produced by a wave form synchronized to the X-axis sawtooth. Sinusoidal wave forms produced standing gratings of arbitrary spatial frequency; pulses produced vertical bars of arbitrary width and horizontal position.

Each spatial wave form was modulated in time by multiplication in an analogue multiplier with the desired temporal modulation signal. This signal was either a sinusoid or square wave produced by the display control, or a sum of sinusoids produced by a digital-to-analogue converter of the 11/20 computer. In either case, a temporal modulation signal of zero annihilated the pattern, and a change in the sign of the modulation signal produced contrast reversal.

The two spatiotemporal products were combined in an analogue multiplexer, which selected the appropriate signal contingent on the value of the Y-axis triangle wave. In this way the multiplexer produced two distinct regions with rectilinear boundaries. Within each region was one of the spatiotemporal visual stimuli.

The spatial configurations used in many of these experiments are shown in Pl. 1. In Pl. 1*A*, *B* and *C* the central region is a rectangular spot whose horizontal extent is fixed by the width of a pulse synchronized to the X-axis sawtooth wave, and whose vertical extent is fixed by a height-control potentiometer in the multiplexer. The four blocks in the periphery of Pl. 1*A* are generated by a pulse of the same sign as the centrally located pulse. The peripheral pulse begins at a fixed time in each sweep and continues until a fixed time in the following sweep. The unpatterned horizontal strip between the upper and lower blocks on each half of the screen is a by-product of the action of the multiplexer. This configuration was the pattern used for the centre plus periphery (c + p) condition.

In Pl. 1*B* a similar configuration is shown, but with the difference that the central and peripheral pulses are opposite in sign. Thus, when the centre spot is above the mean level in luminance, the peripheral spots are all below the mean, and vice versa. The Figure is an instantaneous snapshot of the visual stimulus during a centre minus periphery (c − p) episode (see below).

Pl. 1*C* is a centre spot and a patterned peripheral stimulus. Here a sine grating was formed by gating a sine wave oscillator with the same pulse which formed the spatially uniform peripheral stimulus areas in Pl. 1*A* and *B*. The spatial frequency of the grating could be varied. For all these spatial configurations, the spatial patterns were modulated in time by a sum of sinusoids, as described below. In all the configurations in Pl. 1, the horizontal separation between the peripheral spots could be varied by varying the width (duration) of the peripheral pulse. The vertical separation was determined by the multiplexer, and was equal to the height of the central rectangular spot.

Experimental protocol

The basic experiments on spatial summation were done with the patterns of Pl. 1 and with temporal modulation by a sum of eight sinusoids. The frequencies of the sinusoids were, approximately: 0·21, 0·46, 0·95, 1·92, 3·88, 7·78, 15·6, 31·2 Hz. These particular frequencies were chosen so as to eliminate overlaps of second order with first order frequencies, and to allow phase averaging to cancel out higher order overlaps. An experiment of this type was divided into thirty-two episodes, each about 32 sec in length. There were four basic episodes, repeated eight times. First, the central spot alone was modulated by the sum of sinusoids and the periphery

was held at the mean luminance (the c condition). Secondly, centre and periphery were modulated together, in phase (the c+p condition as in Pl. 1*A*). Thirdly, the periphery alone was modulated and the centre was held at the mean luminance (the p condition). Fourthly, centre and periphery were modulated out of phase (the c−p condition as in Pl. 1*B*). This meant that in the c−p episodes the temporal modulation of the periphery was exactly the negative of the temporal modulation of the centre. The interleaving of c, c+p, p and c−p episodes tended to compensate for any trends in the data due, for instance, to fluctuations in sensitivity of the retina. In most of the experiments reported here, the contrast was 0·05 per sinusoid in the temporal modulation signal. This contrast was chosen to be intermediate in the dynamic range of retinal ganglion cells.

The four basic episodes were repeated eight times. In each repetition the relative phases of the sinusoids within the modulation signal were shifted with respect to one another. This phase shifting within the stimulus allowed cancellation of contamination from high order non-linear interactions when the responses were averaged. This technique is explained in detail in Victor & Shapley (1979). The averaging of the responses from eight episodes of each condition also gave a very high signal-to-noise ratio.

RESULTS

Non-linear summation

Frequency kernels. As in previous work, responses were obtained as Fourier components in the optic tract fibre impulse train. The first order responses were the Fourier components (amplitude and phase) at the input frequencies. Second order non-linear responses were obtained from the Fourier components at harmonic and intermodulation frequencies. This approach has been explained in detail in other papers (Victor *et al.* 1977; Victor & Shapley, 1979). The basic strategy was to choose frequency sets for which first and second order frequencies were distinct, and which permitted higher order overlaps to be cancelled out by the phase averaging mentioned above. This enabled the measurement of accurate first and second order frequency kernels. In this paper we will only be concerned with first order frequency kernels.

The first order frequency kernel $K(f)$ is defined as the set of Fourier components in the response at those frequencies present in the input sinusoidal sum. As such, this kernel is the transfer function, measured at discrete points, of the linear filter which fits best the retinal transductions that produce the optic fibre impulse train. The criterion of best fit is that of least squares. If the retinal network were linear, the first order frequency kernel would be its transfer function. Since we know from previous work (Enroth-Cugell & Robson, 1966; Hochstein & Shapley, 1976*a*, *b*; Victor *et al.* 1977; Shapley & Victor, 1978) that the cat's retinal network contains non-linear stages of transduction, we view the first order frequency kernel as representing the linear part of the network's response to our particular modulation signal.

The purpose of these experiments was the study of integration of neural signals in the retina. Therefore we used visual patterns which stimulated two separate regions of the receptive fields of each retinal ganglion cell. The spatial configuration of the stimuli was as shown in Pl. 1*A* and *B*. The dimensions and position of the central spot were chosen to produce a maximal centre response. The separation of the four outer blocks from the central spot was chosen to optimize the amount of surround antagonism. However, this separation was never less than 0·5 deg, to minimize the effects of blur and scattered light.

Vector summation. The frequency kernel which results from the simultaneous

stimulation of two inputs is defined in the same way as for a single input: as the set of Fourier components of the proper order of combination. For example, the first order kernel is again the set of Fourier components at the input frequencies. But in the present case of two regions which may interact, the first order kernel when two inputs are presented is almost always not simply the sum of the first order kernels when each input is presented alone. In this case non-linear interaction from one region may well affect the first order kernel in the other region, and vice versa. To illustrate this, we show representative vector summation plots (cf. Maffei, Cervetto & Fiorentini, 1970). The values of the first order frequency kernels are complex numbers and so addition and subtraction follow the rules for vector addition

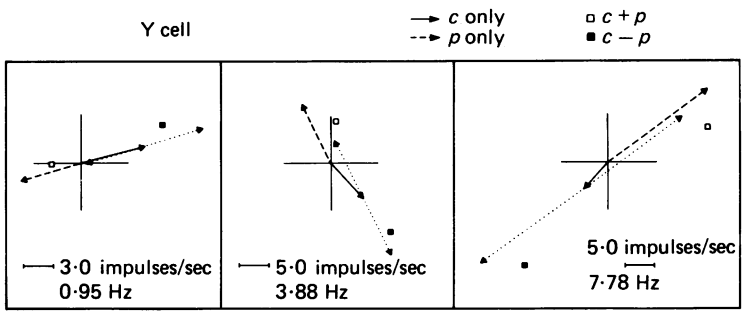


Fig. 1. Vector summation plots for a Y cell. First order responses are plotted as vectors in the complex plane, in which in-phase responses extend horizontally to the right of the origin. Phase advance is counter-clockwise. The spatial configuration was as in Pl. 1*A* and *B*. The response to the centre alone is plotted as a continuous vector. The response to the periphery alone is plotted as a dashed vector. Also shown are the responses to *centre plus periphery* (□) and *centre minus periphery* (■). The dotted vectors are the predicted positions for the vectors of centre plus periphery and centre minus periphery under the assumption of linear summation.

and subtraction. The linear prediction is that $K_{c+p}(f) = K_c(f) + K_p(f)$ and $K_{c-p}(f) = K_c(f) - K_p(f)$ where K_c is the kernel for centre stimulation alone, K_p is for periphery alone, K_{c+p} is for centre and periphery in phase, and K_{c-p} is for centre and periphery out of phase.

Vector summation plots for a typical on-centre Y cell are shown in Fig. 1. The central spot was a $1° \times 1°$ square, and the distance between the central spot and the outer blocks was also 1°. The contrast produced by each sinusoid in the input signal was 0·05. Each vector summation graph of Fig. 1 corresponds to a separate frequency in the input signal. Responses at three input frequencies, 0·95, 3·88 and 7·78 Hz, are chosen for illustration. The continuous vector indicates $K_c(f)$. The dashed vector indicates $K_p(f)$. The dotted vectors indicate the result of adding and subtracting algebraically $K_c(f)$ and $K_p(f)$. The responses actually obtained to the combined stimuli are indicated by the open squares ($K_{c+p}(f)$) and filled squares ($K_{c-p}(f)$). In each case, there is a small but systematic discrepancy between the linear prediction and the actual response. (The data points have a standard error of measurement of less than 1 impulse/sec).

Similar vector summation plots for an on-centre X cell are shown in Fig. 2, at the same three input frequencies. In this case, the central spot measured $0·5 \times 0·9$ deg,

and was separated from the outer blocks by 0·5 deg. Each input sinusoid produced a contrast of 0·05. Again, there is always a discrepancy between the linear prediction and the actual response, although this discrepancy is somewhat less in X than in Y cells.

Effective kernels. These discrepancies were analysed by considering the effective first order kernels of the responses to central and peripheral stimulation. We postulate that the central and peripheral kernels are modified by the simultaneous stimulation of the two areas, but that the modified, or 'effective', kernels are then added to produce the observed responses.

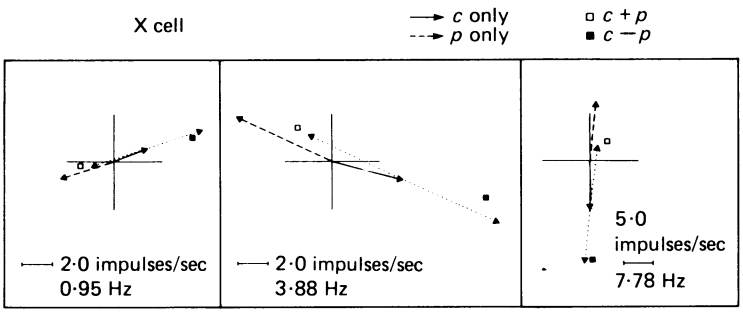


Fig. 2. Vector summation plots for an X cell. Responses are plotted as in Fig. 1. The spatial configuration was that shown in Pl. 1*A* and *B*. The response to the centre alone is the continuous vector. The response to the periphery alone is the dashed vector. Also shown are the responses to *centre plus periphery* (□) and *centre minus periphery* (■). The dotted vectors are the predicted positions for the vectors of centre plus periphery and centre minus periphery under the assumption of linear summation.

The effective frequency kernel of the centre $K'_c(f)$ was defined as half the sum of the kernel of the centre-plus-periphery condition $K_{c+p}(f)$ and the kernel of the centre-minus-periphery condition $K_{c-p}(f)$. That is, $K'_c(f) = 1{\cdot}5(K_{c+p}(f)+K_{c-p}(f))$. Similarly, the effective kernel of the periphery is given by $K''_p(f) = 0{\cdot}5(K_{c+p}(f) - K_{c-p}(f))$. This calculation is illustrated graphically in Fig. 3.

The virtue of these definitions rests primarily on the following consideration. Suppose, for a moment, that interaction of the central and peripheral stimuli were linear. Then the effective frequency kernels $K'_c(f)$ and $K'_p(f)$ would be exactly equal to the frequency kernels of the centre and periphery measured separately, $K_c(f)$ and $K_p(f)$. The amount and nature of the deviation of $K'_c(f)$ from $K_c(f)$ is an index of how stimulation in the periphery affects the first order characteristics of the receptive field centre. Similarly, the departure of $K'_p(f)$ from $K_p(f)$ indicates how much the linear component of the response elicited in the receptive field periphery is affected by temporal modulation in the centre.

The quotients K'_c/K_c and K'_p/K_p. In order to analyse the deviation from linear summation, we considered the quotient of the effective response divided by the isolated response, for example K'_c/K_c. The quotient was a complex number. The amplitude of this complex number indicates whether the presence of the other region enhanced or attenuated the response of the region in question. Its phase indicates the relative phase shift produced by stimulating the other region. The deviation of these quotients from unity expresses the failure of linear summation in

a manner independent of the absolute size or phase shift of the responses. Thus one can compare different cells and also different frequency components in the same cell.

The ratios K'_c/K_c and K'_p/K_p are plotted in Fig. 4. Figs. 4*A* and *B* are derived from the data of the ganglion cells which were the sources of Figs. 1 and 2. For both

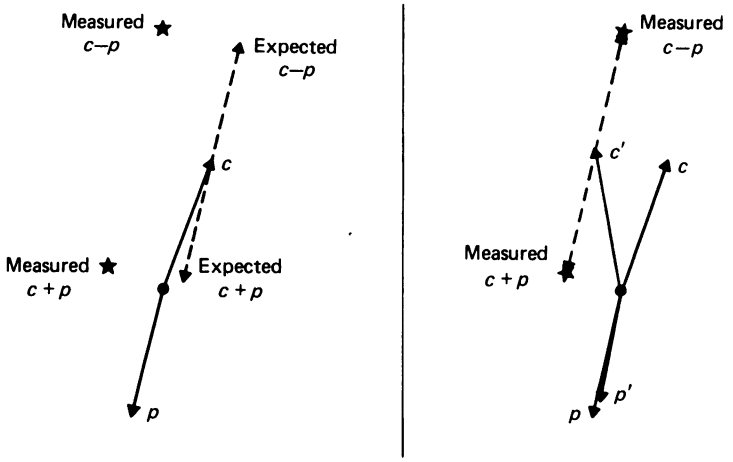


Fig. 3. A graphical calculation of the effective centre and effective periphery responses. Response vectors are shown as vectors in the complex plane, whose lengths indicate amplitude of response and whose orientations indicate phase of response, as in Fig. 1. In the left panel, the dashed lines illustrate the vector sum and difference of the isolated centre and periphery responses, c and p. These deviate from the measured combined responses, $c+p$ and $c-p$ (indicated by the stars). In the right panel, the effective centre and periphery responses, c' and p', are calculated. The effective centre response, c', is defined as the average of the two measured combined responses, $c+p$ and $c-p$. The effective periphery response, p', is defined as one-half of the difference of the two measured combined responses, $c+p$ and $c-p$.

units, it is clear that the ratio K'_p/K_p is essentially unity; the effective response and isolated response of the receptive field periphery are identical in amplitude and phase shift. However, the ratio, effective response/isolated response, for the centre region, K'_c/K_c, differs substantially from unity. In both these cases and in general, the amplitude of the ratio K'_c/K_c is considerably less than unity for low temporal frequencies. Furthermore, the phase shift of the ratio is significantly different from zero for high temporal frequencies. The phase of K'_c always leads the phase of K_c at high temporal frequencies. For the Y cell, the phase effect is clearly larger than for the X cell. Also, there is actually an enhancement of the effective centre response in the Y cell at the highest temporal frequency plotted. This is shown by the fact that the amplitude of K'_c/K_c exceeds unity at this point. Similar data were obtained for off-centre X and Y cells (Fig. 5*A* and *B*). A problem with off-centre cells was that several of them had low or zero mean rate in the absence of stimulation. For such cells, the amplitudes of the responses were poor indicators of retinal interaction. Therefore, we were led to consider the use of the phase shifts of the kernels as a measure of non-linear summation.

The effect of central stimulation on the response of the periphery. Although the effect

of peripheral stimulation on the centre's response was marked and consistent, the effect of central stimulation on the response of the antagonistic surround was in general much smaller (Figs. 4*B* and 5*A*) if not undetectable (Fig. 4*A*). However, in

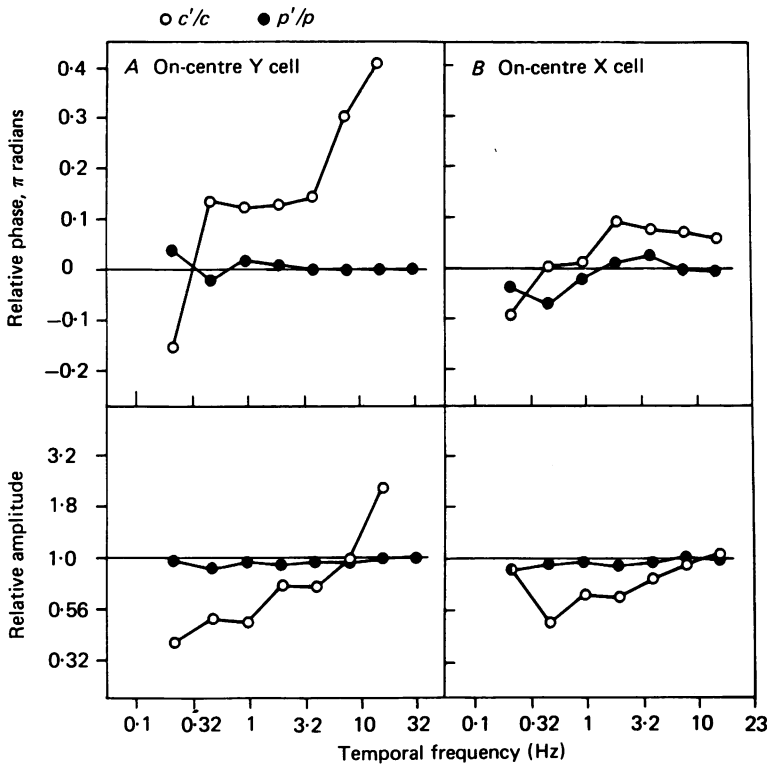


Fig. 4. The ratio of effective kernels to isolated kernels. The graphs display the amplitude and phase of the ratios $K_c'(f)/K_c(f)$ and $K_p'(f)/K_p(f)$ for two ganglion cells; one on-Y, one on-X. The stimulus was as shown in Pl. 1*A* and *B*. The contrast was 0·05 per sinusoid. For each cell, the upper panel shows the phase of the ratio $K_c'(f)/K_c(f)$ (○) and the phase of the ratio $K_p'(f)/K_p(f)$ (●). The lower panel shows the amplitude of the ratio $K_c'(f)/K_c(f)$ (○) and the amplitude of the ratio $K_p'(f)/K_p(f)$ (●). If the summation of centre and periphery were linear, all the phases would have the value zero and all the amplitudes would have the value one. *A*, on-centre Y cell. Both phase and amplitude of the effective centre/isolated centre ratio reveal the effect of non-linear summation. The phase deviates from zero especially at higher frequencies. The amplitude of the ratio is much less than one at low temporal frequencies, but is greater than one at the highest temporal frequencies for which we could measure the response reliably (15·6 Hz). Note that the ratio of the effective peripheral kernel/isolated peripheral kernel had approximately zero phase shift and unit amplitude at all frequencies. *B*, on-centre X cell. A phase advance of the effective centre/centre ratio was also present in X cells at high temporal frequencies. The amplitude of the effective centre/centre ratio was much less than unity at low modulation frequencies, especially at 0·5–1·0 Hz. The effective periphery/periphery ratio had unit amplitude and no consistent phase advances or lags.

a few units, there was an attenuation of the peripheral response by the presence of central stimulation. An example of data from a unit of this sort is shown in Fig. 5*B*. It is seen that the attenuation was approximately uniform over the frequency range used, and was thus qualitatively different from the effect of peripheral stimulation

on the centre's response. The small effect of central stimulation on peripheral response may be due to a non-linearity at the point of impulse generation by the ganglion cell. Indeed, the data do not as yet pass the tests discussed below (ganglion cell non-linearity) that suffice to exclude this possibility as an explanation for the

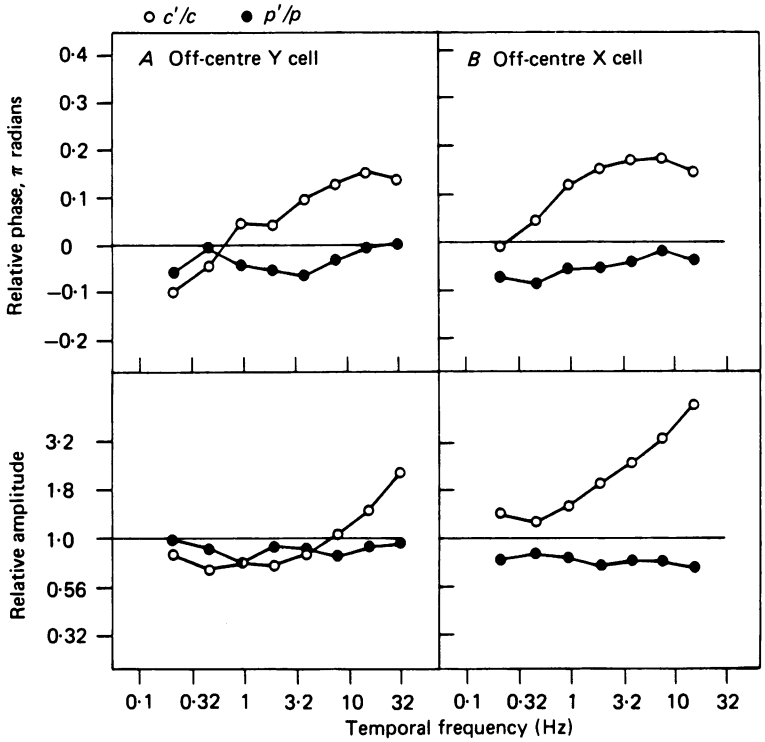


Fig. 5. Effective kernels/isolated kernels in off-centre cells. *A*, off-centre Y cell. The central spot was 2° × 1·5°. The separation between the edge of the spot and each of the peripheral blocks was 0·7°. The contrast was 0·05 per sinusoid. As in Fig. 4, the effects on the effective centre/isolated centre ratio were consistently a phase advance at high frequencies and an amplitude depression at low frequencies. *B*, off-centre X cell. The central spot was 2·5° × 1·9°. The separation between central and peripheral stimulus was 1·3°. The contrast was 0·10 per sinusoid. Here again the main consistent effect was the phase advance of the effective centre/isolated centre ratio at high frequencies. The amplitude data are somewhat hard to interpret because the mean rate was lower in the absence of peripheral stimulation in this cell as in many off-cells. This may explain why the effective centre/isolated centre ratio is so much greater than unity in such cells.

effect of peripheral stimulation on central response. Because the effect of centre on periphery is only present in some cells, and because it is qualitatively different from the effect of the periphery on the centre, we have not yet studied it in detail.

Comparison among cells. To compare the effects of non-linear summation from different units, we chose the phase shift of the effective response/isolated response quotient at the temporal frequency 7·8 Hz as an index of the degree of non-linear spatial summation. Two reasons justified this choice: (1) the first order kernels often peaked at a frequency near 7·8 Hz, so the value of the phase at that frequency is a very reliable number and (2) in general, the effect of non-linear summation on the

amplitude at low frequencies was highly correlated with the effect on the phase shift at 7·8 Hz. Thus the phase shift at 7·8 Hz is essentially equivalent to a measure based on the amplitude depression at, say, 1 Hz.

Fig. 6 displays the phase shift at 7·8 Hz for all twenty-nine X cells (twenty-one on-centre, eight off-centre) and twenty-six Y cells (eighteen on-centre, eight off-

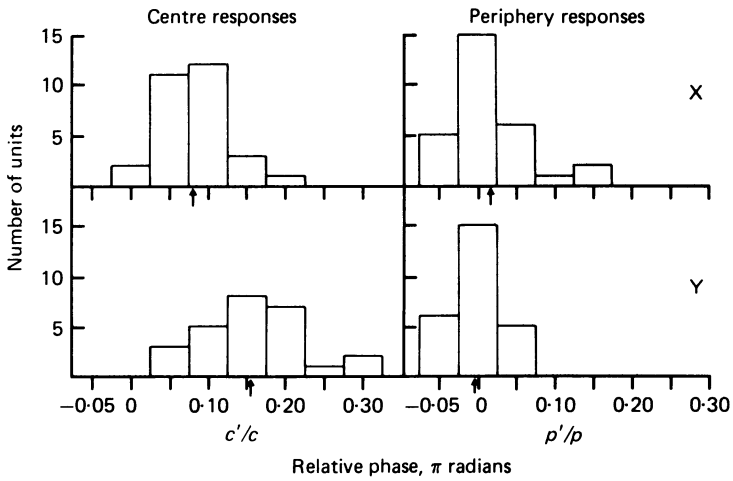


Fig. 6. Population histograms of the phase shift at 7·8 Hz for the effective centre/isolated centre and effective periphery/isolated periphery ratios for X cells and Y cells. All these data were from experiments in which the stimulus configuration was as in Pl. 1*A* and *B*; the modulation signal was a sum of eight sinusoids with a contrast of 0·05 per sinusoid. In each graph the mean of the phase shift is indicated by the arrow.

centre) which we have studied with the centre-periphery stimulus arrangement as in Pl. 1*A* and *B*, and with a contrast of 0·05 per sinusoid in the temporal modulation signal. The phase shift of the ratio effective centre/isolated centre is positive in every one of the units studied. The average advance in Y cells, $0{\cdot}15\pi$ radians (28°), is clearly greater than the average advance in X cells, $0{\cdot}08\pi$ radians (14°). However, the phase of the response to the peripheral stimulus is essentially independent of the presence or absence of the centre stimulus in both cell types: the average phase of the ratio K'_p/K_p is $0{\cdot}017\pi$ radians (3°) for X cells, and $-0{\cdot}004\pi$ radians ($< 1°$) for Y cells.

In a few units, we measured the effective/isolated responses at two contrasts: 0·025 and 0·05. Typical results are shown for an on-centre Y cell in Fig. 7. The absolute amplitudes of the responses at 0·05 contrast were almost double those at 0·025, but the effective centre/isolated centre ratios were practically identical at two contrast levels, both in amplitude and phase.

Modulated patterns in the periphery

Consider the hypothesis that the non-linear summation we see is due to non-linear interaction between the receptive field centre and its classical antagonistic surround (Kuffler, 1953; Rodieck & Stone, 1965). The antagonistic surround should produce

a first order response nearly 180° out of phase with respect to the first order response of the receptive field centre (Maffei *et al.* 1970). If centre–surround interaction were the source of non-linear summation, a necessary prerequisite for non-linear summation between centre and periphery would be the presence of a strong first order response from the antagonistic surround mechanism. We tested this hypothesis by examining the effect of modulated spatial patterns in the periphery. The spatial pattern we used was a sine grating of relatively high spatial frequency as in Pl. 1*C*. It produced no first order (linear) response from the receptive field surround.

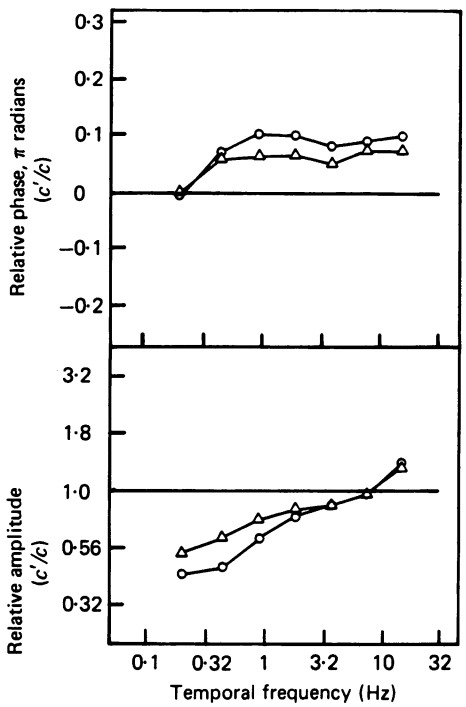


Fig. 7. The effect of contrast on the effective centre/isolated centre ratio. Shown are amplitudes and phases for two experiments on the same on-centre Y ganglion cell: at 0·05 contrast per sinusoid (○) and at 0·025 per sinusoid (△). The stimulus configuration was as in Pl. 1*A* and *B*.

As in our earlier experiments with stimulation of the centre plus and minus the periphery, the experimental procedure was interleaved runs of central stimulation, centre plus periphery, peripheral stimulation, and then centre minus periphery. In this case, the stimulus in the periphery produced no first order responses and so the conditions 'centre plus periphery' and 'centre minus periphery' were essentially repeats. As in the experiments reported above, we quantified the non-linear summation by taking the ratio of the effective central first order kernel, $K'_c(f)$, to the isolated central kernel, $K_c(f)$. The ratio $K'_p(f)/K_p(f)$ had no meaning, since the first order responses to the peripheral stimuli in this case were zero.

The ratio $K'_c(f)/K_c(f)$ for an on-centre Y cell is shown in Fig. 8. The stimulus configuration consisted of a $1{\cdot}2 \times 1{\cdot}2$ deg spot positioned to produce a maximal

centre response, and four blocks in the receptive field periphery, each separated by 1·0 deg from the central spot. In the first set of data, the blocks in the surround were spatially uniform and were modulated with a contrast of 0·05 per sinusoid. In the second set of data, outer blocks consisted of 1 c/deg spatial sine gratings. The modulation contrast was increased to 0·10 per sinusoid, so that the spatial root-

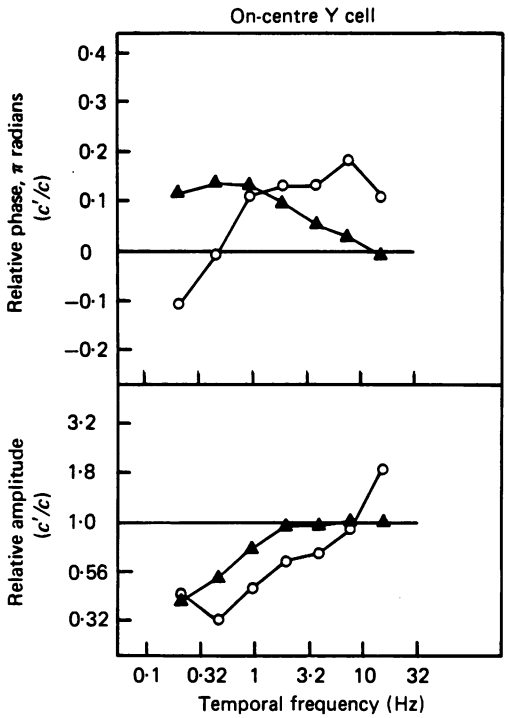


Fig. 8. The effect of a patterned peripheral stimulus compared to a spatially uniform peripheral stimulus. The amplitudes and phases of the $K'_c(f)/K_c(f)$ ratio are plotted for two experiments on one Y on-centre ganglion cell: one experiment with a spatially uniform periphery as in Figs. 4 and 5 (○), the other experiment with a patterned peripheral stimulus, a 1 c/deg sine grating in the periphery (▲). The contrast of the grating was 0·10/sinusoid and the contrast of the central spot was, as in the spatially uniform experiment, 0·05 per sinusoid.

mean-square contrast was the same as in the first set. In both sets of data, the modulation of the centre produced a contrast of 0·05 per sinusoid. With the spatially uniform peripheral stimulus, the ratio effective centre response/isolated centre response (Fig. 8) behaved in the typical manner described above. When the peripheral stimulus was changed to the modulated grating, the peripheral stimulation still affected the over-all linear response. However, the phase advance of the centre response occurred at lower temporal frequencies with the grating as the peripheral stimulus. The amplitude of the first order centre response still showed the characteristic suppression at low temporal frequencies.

As one would expect for a Y cell, the second order frequency kernel obtained with the surround stimulus was substantial, with a peak response of about 5 impulses/sec

(Victor *et al.* 1977). However, under the hypothesis of linear spatial summation, second order responses evoked by peripheral stimulation should not influence the linear response. Nevertheless, one might suppose that the second order response elicited by the stimulation in the periphery was responsible for the alteration of the centre response. This hypothesis can be tested by performing the same experiment

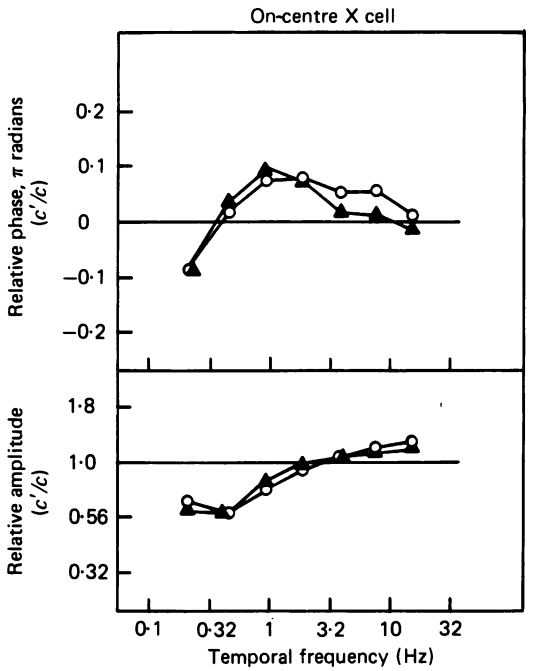


Fig. 9. Patterned peripheral stimulus *vs.* spatially uniform peripheral stimulus for an on-centre X cell. This Figure shows the amplitudes and phases of the effective centre/isolated centre ratio for a spatially uniform periphery (○), and a patterned periphery (▲). The pattern in the periphery was a 0·7 c/deg grating arranged as in Pl. 1*C*. It was modulated by a sum of sinusoids at a contrast of 0·1/sinusoid. The central spot and the spatially uniform peripheral stimulus arranged as in Pl. 1*A* and *B* were modulated by a sum of sinusoids at a contrast of 0·05 per sinusoid. The amplitudes of the first and second order kernels produced by the patterned peripheral stimulus in this experiment were impulse/sec or less.

in an X cell. In such a unit, a fine spatial pattern in the periphery should produce neither a first nor a second order response (cf. Victor *et al.* 1977).

An experiment with a patterned surround on an X cell is shown in Fig. 9. A spatially uniform peripheral stimulus as in Pl. 1*A* and *B* was compared with a 0·7 c/deg grating in the periphery. The central spot stimulus measured 0·8 × 1·0 deg. The separation between the spot and each of the peripheral blocks was 1·8 deg. When the grating in the periphery was modulated with a contrast of 0·05 per sinusoid, the linear responses and the second order responses were negligible. Nevertheless, the peripheral stimulus produced a strong suppression of the centre response. The central response was attenuated by nearly a factor of two at low temporal frequencies (Fig. 9). Furthermore, the modulated grating in the periphery produced

approximately as much phase advance at all frequencies as did the spatially uniform peripheral stimulus. The results of Figs. 8 and 9 are typical for the nineteen ganglion cells we have tested with patterned and spatially uniform peripheral stimuli.

The effects of patterned peripheral stimulation are similar to the effects of modulation over a spatially uniform peripheral area; both kinds of peripheral stimulation

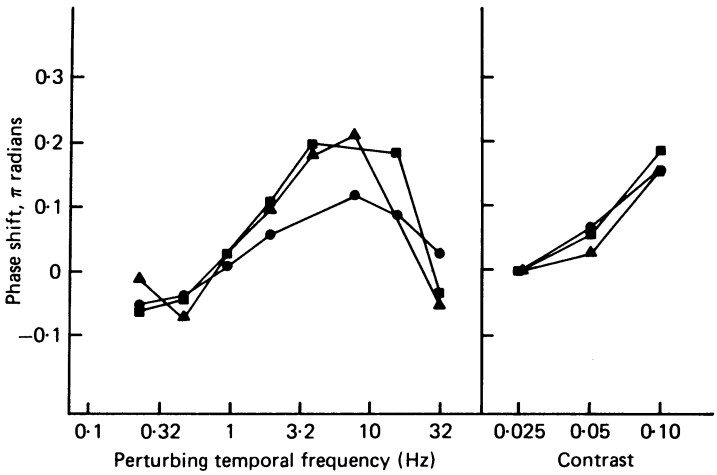


Fig. 10. Two-input perturbation experiments on an on-centre Y cell. The stimulus configuration was as in Pl. 1*A* and *B*. The spatially uniform peripheral stimulus was modulated in time by a single sinusoid at a contrast of 0·1. The central stimulus was 0·9° × 0·9° square spot modulated by seven sinusoids at a contrast per sinusoid of 0·025. The separation between the central spot and the peripheral blocks was 0·8°. The eight frequencies used are specified in Methods. In sequential runs, the perturbing frequency in the periphery was varied and the other seven frequencies in the eight frequency set were used to modulate the centre. The responses which were most affected by the perturbing stimulus were at 3·9, 7·8, and 15·6 Hz. The phase shifts of these responses are shown in the left hand graph: 3·9 Hz (●), 7·8 Hz (■) and 15·6 Hz (▲). The abscissa is the frequency of the perturbing stimulus in the periphery. The right hand graph shows the relationship of the phase shift *vs.* contrast per sinusoid for the central stimulus at each of the three assay frequencies; 3·9 Hz (●), 7·8 Hz (■) and 15·6 Hz (▲). Zero phase in this case is taken as the phase of the response at a contrast of 0·025/sinusoid. For the experiments which generated this graph all eight sinusoids were used to modulate the central spot and all were equal in amplitude.

reduce centre response amplitude at low temporal frequencies, but in Y cells the phase advance produced by the grating in the periphery occurs at lower temporal frequencies.

These experiments prove that non-linear summation is not due to the strength of the response of the antagonistic surround mechanism. Some other receptive field mechanism must be responsible for the non-linear interaction.

The temporal tuning of the non-linear summation mechanism

We have also studied the nature of the influence of peripheral stimulation on the central response by determining which temporal frequencies presented to the receptive field periphery had the greatest effect on the centre. In this way we could

characterize the effective temporal tuning at the input of the non-linear interaction mechanism. We used a direct approach called the two-input perturbation procedure, in which the effects of temporal modulation at single temporal frequencies in the periphery could be tested independently.

The experimental paradigm was as follows. In each episode, a sum of seven sinusoids at low contrast modulated a spot positioned in the centre of the receptive field. The eighth sinusoid modulated four blocks surrounding the central spot at a considerably higher contrast. The seven sinusoids served as an assay of the transfer properties of the centre. Under the hypothesis of linear spatial summation, the response to each sinusoid in the centre should be independent of which one sinusoid was present in the periphery. Contrary to this hypothesis, sinusoidal stimulation at one frequency in the receptive field periphery did affect the response to different frequencies in the centre, as a consequence of the non-linear summation mechanism we have been studying.

Although any variation in the centre response would indicate a non-linearity of spatial summation, variations in amplitude might only be a result of truncation of the impulse rate at zero. Truncation was more of a problem in these experiments than in the earlier experiments with eight frequencies of equal amplitude. However, such a truncation-type non-linearity would by itself have no effect on the phases of the centre response components. Therefore we again chose the variation of the phases of the centre response components as an indicator of more essential types of non-linearity. This had the additional advantage that it allowed a direct comparison with our previous single-input perturbation experiments (Shapley & Victor, 1978).

The results of a two-input perturbation experiment performed on an on-centre Y cell are shown in Fig. 10. For this unit, the central spot was 0·9 deg square, and the distance to the outer blocks, which were spatially uniform, was 0·8 deg. The contrast of each of the sinusoids modulating the central spot was 0·025; the contrast of the single sinusoid modulating the peripheral spots was 0·10. The phases of the centre responses at 3·9, 7·8 and 15·6 Hz are plotted as a function of the frequency of the perturbing sinusoid in the periphery. These phases are plotted as shifts relative to the phases of the response at a central contrast of 0·025 in the absence of peripheral stimulation. It is apparent from the Figure that the responses of the centre are advanced in phase by modulation in the periphery at a wide range of temporal frequencies, and that peripheral stimulation at frequencies near 8 Hz seems most effective in this regard. One also observes that the curves obtained using the phase shifts at different frequencies as assays differ primarily in vertical scale, not peak position.

We also performed the two-input perturbation experiment using a sine grating in the receptive field periphery, rather than a spatially uniform pattern. A comparison between the results obtained with a spatially uniform peripheral stimulus and those obtained with a 1 c/deg grating in the periphery is presented for an off-centre Y cell in Fig. 11. The stimulus configuration consisted of a 1 deg wide vertical strip aligned with the centre of the receptive field, and two 8 deg wide bars in the surround, separated by 1·25 deg from the central strip. The seven sinusoids modulating the central bar were each at a contrast of 0·025. When the peripheral stimulus was spatially uniform, it was modulated at a contrast of 0·10. When the uniform strips

were replaced by 1 c/deg gratings, the contrast was doubled to 0·20, in order to maintain the same root-mean-squared contrast over the region. The results for a spatially uniform peripheral stimulus (Fig. 11*A*) are very similar to those shown in Fig. 10. The maximum phase shifts are produced by frequencies near 8 Hz in the periphery. The curves derived from different assay frequencies differ basically in

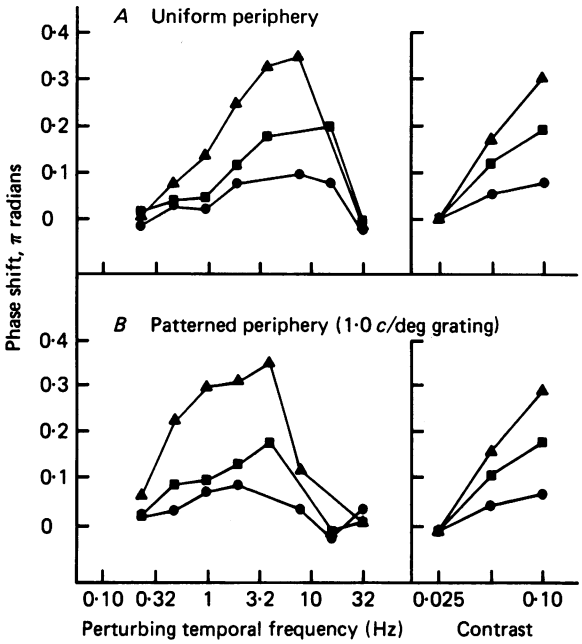


Fig. 11. Two-input perturbation experiments with spatially uniform and patterned periphery in an off-centre Y cell. *A* shows results from an experiment essentially like the one in Fig. 10. In this case the central stimulus was a 1·5° × 20° bar and the peripheral stimulus was composed of two 8·0° × 20° bars modulated together. There was 1·25° separation between the edges of the central bar and the edges of each of the peripheral bars. It can be seen that *A* reproduces all the features of Fig. 10. The assay frequencies were 3·9 Hz (●), 7·8 Hz (■) and 15·6 Hz (▲). The perturbing stimulus in *A* was a single sinusoid at 0·1 contrast. Seven assay frequencies modulated the centre at 0·025 contrast/sinusoid. *B* was an experiment on the same off-centre Y cell but with a 1 c/deg grating in the periphery. The same spatial configuration was used as described above. The assay frequencies were again 3·9 Hz (●), 7·8 Hz (■) and 15·6 Hz (▲). Although the amount of phase advance produced by the perturbing stimulus was about the same as in *A*, the best perturbing stimulus was a modulation frequency lower than was best for the spatially uniform perturbing stimulus. On the right hand panels are plotted the phase shifts of the responses to the central bar modulated at three contrasts: 0·025, 0·05 and 0·10 per sinusoid. The modulation signal in this case was the sum of eight sinusoids of equal amplitude.

vertical scale, not peak position. When the peripheral stimulus was, instead, a 1 c/deg grating, nearly all of the response to the peripheral stimulus was contained at the second harmonic of the input frequency. This is the expected result for patterned modulation of the receptive field periphery in a Y cell (Hochstein & Shapley, 1976*b*). Consistent with results presented above, there was a prominent phase advance, at several assay frequencies, over a wide range of perturbing fre-

quencies of the peripheral stimulation. But there was a clear difference between the patterned peripheral stimulus and the spatially uniform one. The optimal frequency in the periphery for producing a phase shift in the centre response was at 4 Hz for the pattern in the periphery but at 8 Hz for spatially uniform peripheral modulation.

DISCUSSION

The results presented above demonstrate that spatiotemporal modulation in the periphery of the receptive field of a cat retinal ganglion cell modifies the dynamic transfer characteristics of the receptive field centre. This modification of the centre response produces non-linear summation of centrally evoked and peripherally evoked responses in ganglion cells. The spatial and temporal properties of the neural mechanism which underlies this (non-linear) interaction resemble those of the previously identified contrast gain control (Shapley & Victor, 1978). Therefore, we think the action of the contrast gain control is a sufficient explanation for the results presented in this paper. Nevertheless, other mechanisms are conceivable. We will argue against some of these alternative explanations and then will discuss the properties and functional importance of the contrast gain control, as revealed by the present experiments.

Ganglion cell non-linearity and scattered light. The first explanation we will exclude is the proposition that the non-linear summation arises after spatial signals have been combined, in the generation of nerve impulses by the ganglion cell itself. This implies that the ganglion cell applies a non-linear transduction contingent on the magnitude and temporal structure of the neural signal which reaches the ganglion cell from the retinal network. But we have shown that non-linear summation affects equally the response to centre plus periphery *and* the response to centre minus periphery. These two responses are usually quite different in size and temporal structure. Furthermore, if the ganglion cell were responsible, it would have to treat centre and surround signals in the same way. Yet, in our experiments non-linear summation affected the first order responses from the centre systematically, and affected first order responses from the receptive field periphery weakly if at all. The experiments which measured the effect of modulation of a patterned surround on X cells also rule out the ganglion cell as the site for a non-linear transduction. The modulated pattern in the periphery of the receptive field produced no response by itself but nevertheless produced a standard amount of suppression and phase shift on the first order frequency kernel of the centre. Therefore, a whole body of evidence implies that the non-linear interaction takes place within the retina and prior to the generation of ganglion cell impulses.

It is conceivable that scattered light would cause a local non-linearity to masquerade as a non-linearity of spatial summation. However, the experiments with modulated patterns in the receptive field periphery also rule out scattered light as a possible explanation of the non-linear effect of peripheral stimulation on the responses of the centre, because the grating pattern scatters no modulated light onto the centre region.

Relation to previous spatial summation experiments. There is an apparent contradiction between our results and earlier results which showed linear summation of the

responses evoked by centrally and peripherally placed stimuli (Maffei & Cervetto, 1968; Maffei *et al.* 1970; Enroth-Cugell & Pinto, 1970, 1972). We think there may be two separate reasons for this: differences in stimulus configuration and differences in the accuracy of measurement. By using low contrast stimuli and small spots as peripheral stimuli, we have obtained linear summation from ganglion cells (Shapley, R. M., Kaplan, E. & Victor, J. D., unpublished results). This is probably a consequence of the spatial characteristics of the mechanism which underlies the non-linear spatial summation (see below). But perhaps the more significant reason is the greater accuracy of the frequency kernel technique (Victor *et al.* 1977). For example, our procedures permit determination of phase to within about $0{\cdot}03\pi$ radians, which corresponds to ~ 2 msec at 7·8 Hz.

Relation to the effect of contrast on transfer properties

Now we wish to consider what is required to explain the non-linear summation observed in our experiments. Previously, we have described a non-linear effect of retinal contrast on the transfer properties of both X and Y retinal ganglion cells in response to spatial gratings (Shapley & Victor, 1978). We showed that increasing the contrast of the stimulus caused the low-frequency components of the first order frequency kernel to be suppressed relative to the high-frequency components. Concomitantly, the phase shifts of the high-frequency responses showed a consistent advance with increasing contrast. This non-linear effect depended on the contrast of a grating but was independent of the spatial phase of the grating stimulus, and hence independent of the response size of the unit under study. A natural consequence of the spatial phase invariance of the non-linear effect of retinal contrast is non-linearity of spatial summation; the presence of a peripheral stimulus (with any phase relationship to the centre stimulus) increases the total retinal contrast; thus the centre's contribution to the combined response would be generated at a higher contrast than its response in isolation.

There is good agreement between the qualitative features of non-linear summation and the contrast effect (Shapley & Victor, 1978). The similarities are: (1) presence of the peripheral stimuli causes centre responses to be *relatively* greater at high temporal frequencies than at low temporal frequencies, as does increasing the contrast of a grating stimulus; (2) in both circumstances, there is a consistent phase advance at the high temporal frequencies; (3) over the entire range of assay frequencies and perturbing frequencies, results of the two-input perturbation experiments are similar to the results of the single-input perturbation experiments (Shapley & Victor, 1978). In particular, the data in Figs. 10 and 11 show that the flicker of coarse patterns at frequencies in the 4–15 Hz range are optimal for producing non-linear summation (cf. Fig. 6 of Shapley & Victor, 1978) and that lower temporal frequencies are more effective with finer patterns; (4) the effect of non-linear summation on the phase shift at 8 Hz is about twice as great in Y as in X cells. This parallels the greater effect of contrast on Y cells.

Mechanisms of interaction

The qualitative features of the data presented here can be explained by the general model we have previously introduced to explain the contrast effect (Shapley

& Victor, 1978). The model is shown diagrammatically in Fig. 12. In this model, I_D represents the input to the radial retinal pathways. The filter L represents the classical centre and surround mechanisms of the ganglion cell receptive field (Kuffler, 1953; Rodieck & Stone, 1965), which is assumed to be approximately linear. The first order transfer properties of L are assumed to have a (non-linear) parametric dependence on an auxiliary signal I_C, a measure of the average retinal contrast over

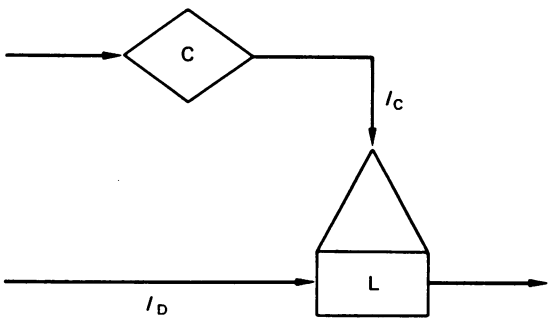


Fig. 12. Model for the contrast gain control. In this model it is assumed that the radial pathways in the retina, represented by I_D and the filter L, are approximately linear at one contrast, but are modified as contrast changes by the contrast sensing network C. The contrast signal from C, denoted I_C, changes the dynamic properties of L at higher retinal contrasts so as to reduce the sensitivity to low frequencies of modulation and to advance the phase at high frequencies of modulation.

a wide area. The contrast network C is composed of subunits which are similar, if not identical, to those that generate the second order excitatory non-linearity of Y cells (Hochstein & Shapley, 1976*b*; Victor *et al.* 1977), because of similar spatial and temporal properties. While the non-linear excitatory effect of the subunits seems confined to Y cells, their modulatory effect on 'linear' transfer properties extends to both X and Y cells. The mechanism of the modification of L by the contrast signal I_C must be rather complex and probably involves shunting membrane resistances or altering strengths of inhibitory feedbacks or both. This two-input model explains the result that a modulated grating in the periphery of an X cell produced no response whatsoever when presented alone, but did alter the response to a central spot (Fig. 9).

Dynamics of the contrast gain control. We can infer the temporal tuning of the front end of the contrast network, C, from the results of the two-input perturbation experiments. The amount of phase shift *vs.* perturbing frequency (Figs. 10 and 11) gives a semi-quantitative estimate of the temporal frequency response of the contrast network. It is significant that these graphs are contingent on the spatial pattern of the perturbing stimulus (Fig. 11). This shift in the temporal frequency response with pattern is analogous to the effect of lateral inhibition (Ratliff, Knight & Graham, 1969; Brodie, Knight & Ratliff, 1978). This behaviour suggests a centre-surround organization built into the subunits of the contrast network C.

Within the contrast network C, there must be a non-linearity of even order so as to make the network sense contrast, and not illumination. Following this non-

linearity is a filter which pools the outputs of the many non-linear subunit mechanisms and delivers the contrast signal I_C to the points in the retina where I_C modifies the dynamics of the radial pathways.

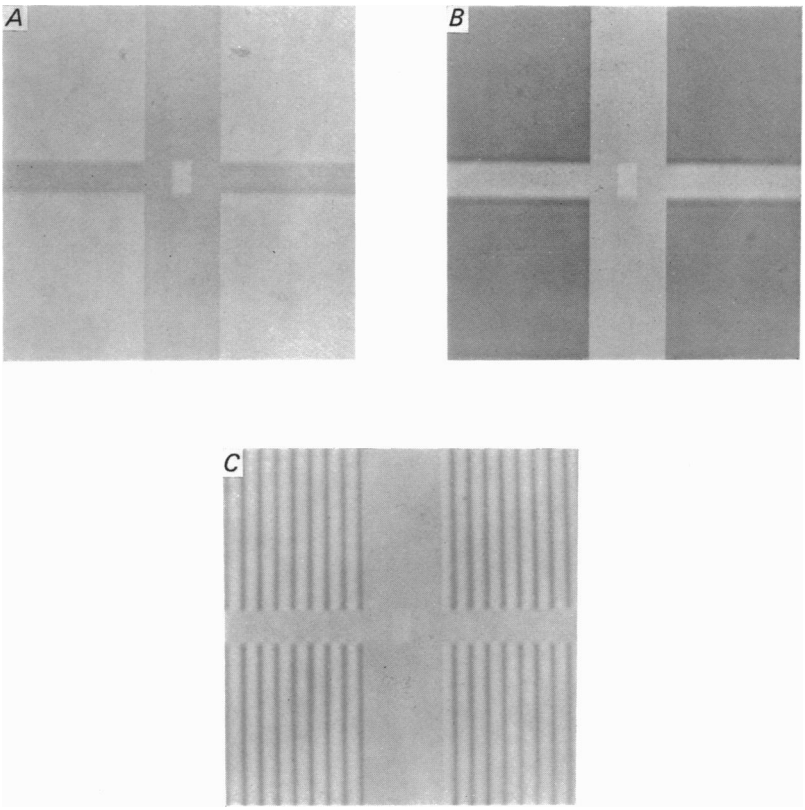
The dynamic characteristics of this last filter are hypothetical. Several of our results are consistent with the hypothesis that the final filter's output, I_C, is a relatively steady level. The invariance of the perturbation effect curves with different assay frequencies suggests that a single parameter of the contrast signal, its constant level, determines their shape. The invariance of the dynamics of the non-linear summation effect with spatial pattern in X cells (Fig. 9), also suggests a dependence on the steady value of I_C. However, in Y cells, the dynamics of the non-linear summation effect depends on the spatial pattern in the periphery (Fig. 8). Thus, at least in Y cells, there must be temporal modulation of the contrast signal I_C. Furthermore, there may be a basic difference in the way X and Y cells are connected to the contrast network: the contrast signal may have to pass through an additional stage of temporal integration before it affects the first order pathway of the X cell.

Asymmetry of non-linear spatial summation. That stimulation in the receptive field periphery had a marked effect on centre response, but not vice versa, is explained by the spatial configurations we used and the model of Fig. 12. Since the central stimulus was always very small relative to the peripheral stimulus, it probably had only a meagre effect on the contrast signal, I_C. This is because the spatial profile of the network C must be relatively wide and shallow, as implied by previous experiments on the spatial-phase invariance of the contrast effect (Shapley & Victor, 1978).

The 'suppressive surround' and the contrast gain control

Other investigators have discovered 'silent' or 'suppressive' surrounds in a variety of vertebrate retinae. For example, H. B. Barlow's work on the frog retina (Barlow, 1953) demonstrated a silent surround in frog 'on-off' ganglion cells. Recently, this same phenomenon has been found in cat retinal ganglion cells (Cleland & Levick, 1974; Jakiela, 1978 and personal communication). Jakiela's work is particularly relevant to ours since he found that the step response of a ganglion cell becomes more transient in the presence of a drifting grating in the receptive field periphery. His findings are predicted by the changes in the first order frequency kernels we have measured in which low temporal frequency responses are suppressed but higher temporal frequency responses are unaltered or enhanced in amplitude, and speeded up. Thus, the functional importance of the contrast gain control must be to weaken the retina's response to slow variation and to accentuate even more the retina's tendency to respond to change in the visual environment.

The site of this contrast gain control in the retina may be inferred from studies on the mudpuppy retina by Werblin and his colleagues (Werblin, 1972; Werblin & Copenhagen, 1974). They showed that a mechanism for adaptation to 'change', which we have called 'contrast', is present at the amacrine level of the mudpuppy retina, and not prior to this stage. From their experiments, one may conclude that the contrast gain control in mudpuppy is composed of spatial subunits and is spread over a wide retinal area as in the cat retina. The functional similarities between the cat and mudpuppy retinal contrast gain controls suggests a common retinal locus among the amacrine cells.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B
C

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EXPLANATION OF PLATE

PLATE I

Photographs of the stimulus configurations. *A*, centre plus periphery. A small central spot surrounded by four large spatially uniform peripheral areas constituted the centre plus periphery stimulus. The four peripheral areas were all modulated together in phase with the centre. The picture shows an instant of the stimulus when central and peripheral stimuli were above the mean illumination (20 cd/m^2 in most experiments). *B*, centre minus periphery. In this case the four large peripheral areas were modulated exactly out of phase with the centre so that the centre luminance is above the mean while the peripheral luminance is below the mean. *C*, centre plus patterned periphery. In this arrangement the peripheral stimulus was a 1 c/deg sine grating gated by the same pulse which produced the four spatially uniform areas in 1*A* and *B*.