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SPATIAL SUMMATION IN THE RECEPTIVE FIELDS OF SIMPLE CELLS IN THE CAT'S STRIATE CORTEX

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SUMMARY

1. We have examined the responses of simple cells in the cat's striate cortex to visual patterns that were designed to reveal the extent to which these cells may be considered to sum light-evoked influences linearly across their receptive fields. We used one-dimensional luminance-modulated bars and gratings as stimuli; their orientation was always the same as the preferred orientation of the neurone under study. The stimuli were presented on an oscilloscope screen by a digital computer, which also accumulated neuronal responses and controlled a randomized sequence of stimulus presentations.

2. The majority of simple cells respond to sinusoidal gratings that are moving or whose contrast is modulated in time in a manner consistent with the hypothesis that they have linear spatial summation. Their responses to *moving* gratings of all spatial frequencies are modulated in synchrony with the passage of the gratings' bars across their receptive fields, and they do not produce unmodulated responses even at the highest spatial frequencies. Many of these cells respond to temporally modulated *stationary* gratings simply by changing their response amplitude sinusoidally as the spatial phase of the grating is changed. For these neurones, there are two 'null' phases, 180° apart, at which the grating elicits no response: a smaller number of simple cells, all of which have odd symmetric receptive fields, have no 'null' phases for stationary sinusoidal gratings; rather, the temporal phase and amplitude of their response varies in a complicated manner as the spatial phase of the grating is varied. Nonetheless, their behaviour appears to indicate linear spatial summation, since we show in an Appendix that the absence of a 'null' phase in a visual neurone need not indicate non-linear spatial summation, and further that a linear neurone lacking a 'null' phase should give responses of the form that we have observed in this type of simple cell.

3. A minority of simple cells appears to have significant non-linearities of spatial summation. These neurones respond to *moving* gratings of high spatial frequency with a partially or totally unmodulated elevation of firing rate. They have no 'null' phases when tested with *stationary* gratings, and reveal their non-linearity by giving responses to gratings of some spatial phases that are composed partly or wholly of even harmonics of the stimulus frequency ('on–off' responses).

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4. We compared simple receptive fields with their sensitivity to sinusoidal gratings of different spatial frequencies. *Qualitatively*, the most sensitive subregions of simple cells' receptive fields are roughly the same width as the individual bars of the gratings to which they are most sensitive. *Quantitatively*, their receptive field profiles measured with thin stationary lines, agree well with predicted profiles derived by Fourier synthesis of their spatial frequency tuning curves.

INTRODUCTION

In 1962, Hubel & Wiesel provided the first adequate description of the visual responses of neurones in the cat's primary visual cortex, area 17. Using a relatively simple set of geometric test stimuli and classification criteria, they were able to divide striate neurones into two groups, simple and complex. Simple cells have receptive fields that are, like those of neurones in the retina and lateral geniculate nucleus, divided into distinct excitatory and inhibitory regions. Tested qualitatively, simple cells behave as though there is spatial summation within each of these regions, and antagonism between regions of opposite sense. Thus the response elicited by a light presented in an 'on' region increases as the size or intensity of the test pattern increases, and is attenuated or eliminated when the pattern invades an 'off' region. Complex cells, on the other hand, do not usually have distinct regions in their large receptive fields; rather, this field appears more or less uniform, and commonly gives 'on-off' responses to stimuli presented anywhere within it. While the geometry of the optimal spatial stimulus for a simple cell can be predicted from the arrangement of receptive field regions, the optimal stimulus for a complex cell cannot be predicted in this way. The best simply shaped stimulus for a simple cell is one that roughly fills the most sensitive region of its receptive field, while that for a complex cell is usually smaller than the receptive field, or any directly definable receptive field subregion. Simple cells may therefore sum inputs from all parts of their receptive fields in a linear manner, while complex cells cannot act in this way.

Since 1962, many workers have studied the stimulus-selectivity of visual cortical neurones, but there has been no quantitative examination of the basis of Hubel & Wiesel's classification: spatial summation. This property has, however, been extensively studied in more peripheral visual neurones, and a particularly elegant set of tests of spatial summation was devised and used by Enroth-Cugell & Robson (1966) in their study of cat retinal ganglion cells. These techniques have been successfully applied to neurones in the cat's lateral geniculate nucleus (Shapley & Hochstein, 1975), and we now report the results of using them, and other related techniques, to study the receptive field properties of neurones in the primary visual cortex.

Enroth-Cugell & Robson divided retinal ganglion cells into two groups, X cells and Y cells, on the basis of their responses to sinusoidal gratings. They showed that X cells sum influences from all parts of their receptive fields in a linear manner, while Y cells are non-linear in this respect. Their observations have been confirmed and extended by Hochstein & Shapley (1976*a*, *b*), who have examined the nature of the non-linear operations performed by Y cells in more detail. Sinusoidal grating stimuli have been employed in several studies of visual cortical neurones (Cooper & Robson, 1968; Campbell, Cooper & Enroth-Cugell, 1969; Maffei & Fiorentini, 1973;

Ikeda & Wright, 1975*a*, *b*), but these workers have been concerned with defining the selectivity of cortical cells for the parameters of grating stimuli, rather than with using the analytical techniques that these stimuli allow. None of these groups used the powerful techniques of Fourier analysis to interpret their data, or to relate neuronal responses to gratings with those to simpler types of geometric stimuli; it is this power that we wished to exploit in order to reveal some of the operational characteristics of cortical neurones.

In this paper, we examine whether simple cells can be considered to sum inputs from different parts of their receptive fields linearly. In the second paper, we analyse the properties of complex cell receptive fields in order to understand the non-linearities found in spatial summation (Movshon, Thompson & Tolhurst, 1978*a*). The third paper (Movshon *et al.* 1978*b*) compares the preferences of simple and complex cells for sinusoidal gratings of different spatial frequencies, and also compares the properties of neurones in areas 17 and 18 of the visual cortex. We have briefly reported some of our results elsewhere (Movshon & Tolhurst, 1975*a*, *b*).

METHODS

Surgical preparation and maintenance. Adult cats (2–4 kg) were anaesthetized with halothane (Fluothane, I.C.I.). Following venous cannulation, surgery was carried out under a short acting barbiturate (Brietal sodium, Lilly) or steroid (Althesin, Glaxo) anaesthetic given intravenously as needed. Light anaesthesia was maintained during recording with a mixture of $N_2O/O_2/CO_2$ (approximately 78:20:2). Eye movement was minimized with a continuous infusion of gallamine triethiodide (Flaxedil, May and Baker: 10–30 mg/kg.hr) in 6% glucose–Ringer solution (2–3 ml./hr), together with bilateral division of the cervical sympathetic trunks. Body temperature was maintained near 37 °C with a thermostatically controlled heating pad. E.e.g. and e.c.g. were monitored continuously, and peak expired CO_2 concentration was checked at intervals with an infra-red medical gas analyser, and maintained between 4·0 and 5·0% by adjusting the stroke volume of the respiration pump. In some experiments, arterial blood pressure was monitored via a cannula placed in the femoral artery, and maintained in the range 100–160 mmHg by manipulation of respiration parameters and, when needed, small doses of appropriate vasoactive drugs.

Optics. The pupils were dilated with homatropine sulphate, and lids and nictitating membranes retracted with phenylephrine HCl, both applied topically. The corneas were protected with zero-power contact lenses containing 3 mm artificial pupils; supplementary lenses, chosen by direct ophthalmoscopy, were used when necessary to make the retinae conjugate with a screen 114 cm distant. Occasional clouding of the cornea during the later stages of an experiment was resolved by the application of 3% saline, or by scraping the corneal epithelium with a blunt scalpel blade.

Recording. Single units were isolated in area 17 with tungsten-in-glass micro-electrodes (Levick, 1972) having a conical uninsulated tip between 10 and 20 μm in length. The electrode was driven into the cortex through a sealed chamber over a small craniotomy and durotomy (1–2 mm) placed near Horsley–Clarke co-ordinates P6, L2. Action potentials were conventionally amplified and displayed on a storage oscilloscope; a standard pulse triggered by each impulse was heard over an audiomonitor during receptive field mapping and during the setting of contrast thresholds. We did not accept signals less than three times the amplitude of the noise level, and most were much larger. When we were in doubt about the cortical area of our electrode penetrations, we made small electrolytic lesions at points along the track by passing direct current (5 μA, 5 sec, tip negative) through the electrode, and then killed the animal at the end of the experiment with an overdose of Nembutal and perfused it through the heart with 10% buffered formalin. The brain was sectioned at 40 μm and stained with cresyl violet to allow reconstruction and cytoarchitectonic verification of the position of the electrode track.

Receptive field mapping. The receptive fields of each unit were initially plotted by hand on a tangent screen with flashed and moving slits, bars, edges and spots, and classified by the criteria of Hubel & Wiesel (1962) as discussed by Movshon (1975, 1976). In these papers, we concern

ourselves solely with the behaviour of simple and complex cells; the other, more rarely encountered types of unit found in the cortex were excluded. Receptive fields were initially mapped using the 'minimum response field' method described by Barlow, Blakemore & Pettigrew (1967), and marked on graph paper for permanent records. Cells that were responsive to flashed stimuli (the great majority of our sample) were carefully mapped into 'on', 'off' and 'on–off' regions using thin lines, and the sizes of these regions marked on the receptive field maps. Cells that had receptive fields divided into two or more 'on' or 'off' regions were tested with flashed slits of different widths in order to classify them as simple or complex; we did encounter several complex cells with subdivided receptive fields, of the kind described by Hubel & Wiesel (1962).

The positions of the *areae centrales* were projected on to the tangent screen with a reversible ophthalmoscope around the time each receptive field was plotted; these plots were used to estimate the retinal eccentricity of each unit. Most of our sample of units had receptive fields centred within 3° of the *area centralis*, and all of those we discuss in this and the following paper were within 6°. All quantitative analysis was undertaken through the eye that was more effective in driving the unit, and the other eye was covered.

We used a PDP 11/20 digital computer to control each experiment, deliver visual stimuli and accumulate neuronal responses, using methods that we have briefly described elsewhere (Movshon & Tolhurst, 1976).

Visual stimuli were generated by the computer on the face of a display oscilloscope designed and built by J. G. Robson. The display subtended $10 \times 12{\cdot}5°$ at the cat's eye, and had a mean luminance of 150 cd/m^2 (P31 phosphor). We used a television technique derived from that described by Schade (1956) to produce one-dimensional luminance modulated patterns, such as bright and dark bars, edges and gratings of abitrary luminance profile; the frame rate of the display was 128 Hz. At the beginning of each frame, a signal from the oscilloscope interrupted the computer, which then read through a stored list of numbers at about 60 kHz. These numbers were transferred to a digital-to-analogue converter (DAC) whose output controlled the intensity of the writing beam. Each number in this *spatial list* determined the luminance of a strip of the oscilloscope face 10° long and 2′ wide; the display was composed of 400 such strips, each of which was too fine to be resolved by any of the units in our sample or by the cat itself (Bisti & Maffei, 1974; Blake, Cool & Crawford, 1974).

A second list of numbers, the *temporal list*, allowed us to vary the contrast of the display as a function of time. A number from this list was transferred to a second DAC at the beginning of each display frame, and the outputs of the two DACs were multiplied electronically before being sent to the oscilloscope. The spatial pattern defined by the spatial list could be turned on and off, or time-modulated with any wave form. Patterns of constant contrast that moved across the oscilloscope face were produced by offsetting, for each frame, the point at which the computer started to read the spatial list.

Control of over-all stimulus contrast was obtained by routing the signal to the oscilloscope through a programmable logarithmic attenuator; when contrast threshold settings were made, the experimenter controlled this attenuator through the computer's digital inputs.

The display was centred on the receptive field being studied and its orientation carefully adjusted to match the preference of the unit. We varied neither length nor orientation of our stimuli after this; all our experiments were designed to perform a one-dimensional receptive field analysis along a line orthogonal to the unit's preferred orientation.

Neuronal responses to the visual stimuli were compiled into conventional averaged response histograms (Gerstein & Kiang, 1960). A standard pulse triggered by each action potential was routed to the counter input of the computer's clock; during the flyback intervals between display frames, the counts that had accumulated were added to the appropriate bin of a histogram stored in the computer's memory.

Experimental design. The responses of striate cortical neurones are rather variable, and much of this variability is due to slow changes in responsiveness over periods of a few minutes. It is therefore perilous to make quantitative comparisons among response measurements made at different times. Since we wished to compare the relative effectiveness of different visual stimuli, we adopted a version of the multi-histogram technique devised by Henry, Bishop, Tupper & Dreher (1973). All the different visual stimuli we wished to compare were presented in random order several times in one experiment, and separate response histograms accumulated for each. Each experiment consisted of a number of blocks of trials (usually five or ten). In each block, all stimuli were presented in random order, each for a few repetitions (between five and twenty),

and response histograms compiled. The order of the stimuli was newly randomized for each block of trials, and the histograms related to each stimulus added appropriately to those in memory. In this way we could obtain accurate measurements of the relative effectiveness of up to forty different stimuli.

For determination of contrast thresholds, we used a slightly different method (Tolhurst & Movshon, 1975). Instead of accumulating response histograms for each stimulus, the computer permitted the experimenter to adjust the contrast of each stimulus until he judged that it elicited a liminal response from the neurone. He then signalled that the trial was complete, and the computer recorded the attenuation and started presentation of the next stimulus. We normally presented four randomly ordered sequences of the stimuli being compared, obtaining four independent estimates of threshold. The standard error of the mean of these estimates was normally between 0·1 and 0·2 log units, a value only slightly greater than that obtained from a human observer setting his own contrast thresholds under similar conditions.

RESULTS

We recorded from 164 units in twenty-one cats. Of these, sixty-six simple cells and fifty complex cells were analysed quantitatively; the remaining units were either judged insufficiently stable for long-term analysis, or fell into one of the other classes of unit that are found in the striate cortex (see Methods).

On the basis of our qualitative and quantitative receptive field maps, we divided simple cells into two groups: odd symmetric (53: 62%) and even symmetric (32: 38%). An even symmetric simple cell has a single excitatory or inhibitory region in the centre of its receptive field, flanked by two weaker antagonistic regions of roughly equal strength. An odd symmetric simple cell has two side-by-side antagonistic regions of nearly equal strength, which may in turn be flanked by weaker antagonistic regions (Hubel & Wiesel, 1962). This categorization may be to some extent artificial, since receptive fields with intermediate properties certainly exist.

In the first part of this paper, we describe the responses of simple cells to moving and stationary sinusoidal gratings to provide an initial description of the linear and and non-linear behaviour they exhibit. We then present data on their responses to single stationary bright and dark bars presented at different positions on their receptive fields, and compare these responses with those predicted by Fourier analysis from their sensitivity to sinusoidal gratings of different spatial frequencies.

Responses to sinusoidal gratings

Wave form of response to moving gratings

A sinusoidal grating moving laterally at a constant velocity is a stimulus that contains one temporal frequency, the frequency with which the cycles of the grating pass an arbitrary point on the screen.

The luminance of each point in the stimulus changes sinusoidally as each cycle of the grating moves past; different points on the screen differ only in the phase of this luminance modulation. The response of a linear visual neurone to such a stimulus should contain only the temporal frequency at which the stimulus moves. The response wave form should be sinusoidal, and the mean level of activity should be unaltered.

However, striate cortical neurones rarely have much maintained discharge (Pettigrew, Nikara & Bishop, 1968; Rose & Blakemore, 1974), so that the averaged

response of a linear neurone should be a rectified sine wave, the neurone being silent for about half the stimulus cycle.

Fig. 1 illustrates the responses of two simple cells to moving sinusoidal gratings of various spatial frequencies. For cell A, each response histogram showed only one peak, and for more than half the cycle the neurone was silent. There were thus no obvious non-linearities of spatial summation, apart from the rectification that we have chosen to regard as reflecting the activity of a non-linear output device showing threshold behaviour. Closer inspection of the records reveals a rather unusual behaviour for which we have no explanation: the responses to gratings of very low spatial frequency appear to occupy less of the stimulus cycle than do those to gratings of higher spatial frequency. This behaviour was common in simple cells,

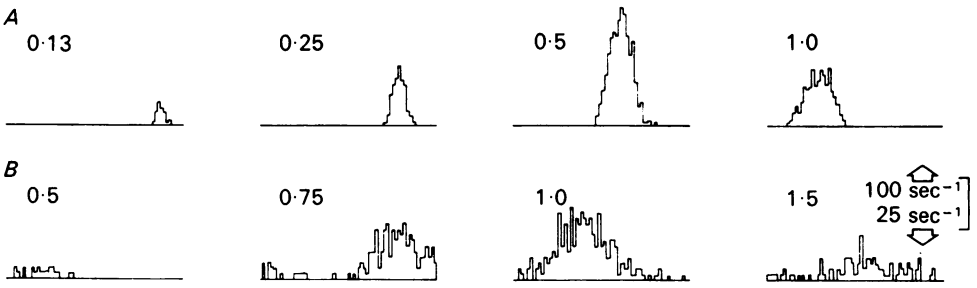

Fig. 1. The responses of two simple cells to sinusoidal gratings of different spatial frequencies, moving over their receptive fields at 2 Hz. Each histogram represents the average response of the neurone to the passage of one cycle of the grating across its receptive field; the number above each histogram indicates the grating's spatial frequency in cycles per degree. The contrast of all the gratings was 0·5. Neither neurone had any maintained discharge in the absence of stimulation.

and might reflect a subthreshold shift in mean membrane current, which would be a non-linearity. This explanation is unlikely, in view of the levels of mean membrane current that it would imply; this behaviour is more likely to reflect a non-linearity of output processing (like the rectification) of the kind we have chosen to ignore. Of forty-seven simple cells tested with drifting gratings, thirty-two (68 %) behaved as if spatial summation were linear; although some of the cells that we have classified as showing linear summation did have different 'widths of response' at different spatial frequencies.

Fifteen simple cells (32 %), showed obvious non-linearities other than rectification, and the responses of one such cell are shown in Fig. 1*B*. For gratings of low spatial frequency, the responses of this cell were similar to those of the linear simple cell shown in Fig. 1*A*, but at medium and high spatial frequencies, the response wave form changed. At no point during the stimulus cycle was the cell silent, and the underlying changes in membrane current cannot have taken the form of a modulation about the mean level without some change in that mean. In fact, at the highest spatial frequency, the response consisted largely of an unmodulated increase in firing, a behaviour reminiscent of Y type retinal ganglion cells (Enroth-Cugell & Robson, 1966).

The extent to which a neurone's response is modulated by a repetitive stimulus may most accurately be determined by Fourier analysis of its response wave form into component sinusoids. We may obtain an objective estimate of the degree to

which a response is composed of modulated and unmodulated components by computing a quantity we term *relative modulation*: which is the ratio of the amplitudes of the response component at the fundamental frequency (f_1) and the zero-frequency response component (f_0) (the latter is the change in mean firing caused by the stimulus).

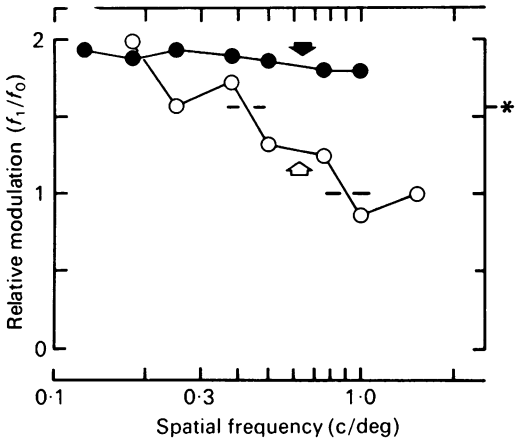

Fig. 2. Graph showing the relative amplitudes of modulated and unmodulated components in the responses of two simple cortical neurones to moving gratings of different spatial frequencies. Relative modulation was determined by calculating the frequency components of the neurones' average responses by Fourier analysis, and then by dividing the amplitude of the component corresponding to the frequency of movement (f_1) by the amplitude of the component at zero frequency (f_0). The asterisk on the ordinate indicates a value of 1·57, which corresponds to the value obtained for a precisely half-wave rectified sine wave. The two cells are those whose responses are illustrated in Fig. 1, filled symbols for the neurone of Fig. 1*A*, open symbols for the neurone of Fig. 1*B*.

Fig. 2*A* plots relative modulation as a function of spatial frequency for the two simple cells whose responses are shown in Fig. 1. The linear simple cell (Fig. 1*A*) is represented by filled symbols; the non-linear simple cell (Fig. 1*B*) is represented by open symbols; the optimum spatial frequencies for these two cells are indicated by the filled and open arrows, respectively. The two levels of relative modulation indicated by horizontal brackets represent the level expected from a neurone showing precise half-wave rectification (1·57, asterisk on the ordinate), and the level below which the unmodulated response component dominates (1·0). The half-wave rectification level is the lowest value of relative modulation compatible with the linearity hypothesis in a neurone lacking maintained discharge; a level of 1·0 or below indicates that there was no rectification in the response wave form, and that there was some firing at all points in the stimulus cycle.

Fig. 2 reveals that the response of the linear simple cell was apparent over less than half the stimulus cycle to gratings of all spatial frequencies tested, having relative modulation values in excess of 1·8. The non-linear cell, on the other hand, gave responses over more than half the cycle to the four highest spatial frequencies tested; at the highest spatial frequency, the zero-frequency response component was dominant. It is important to note that in the vicinity of the optimum spatial

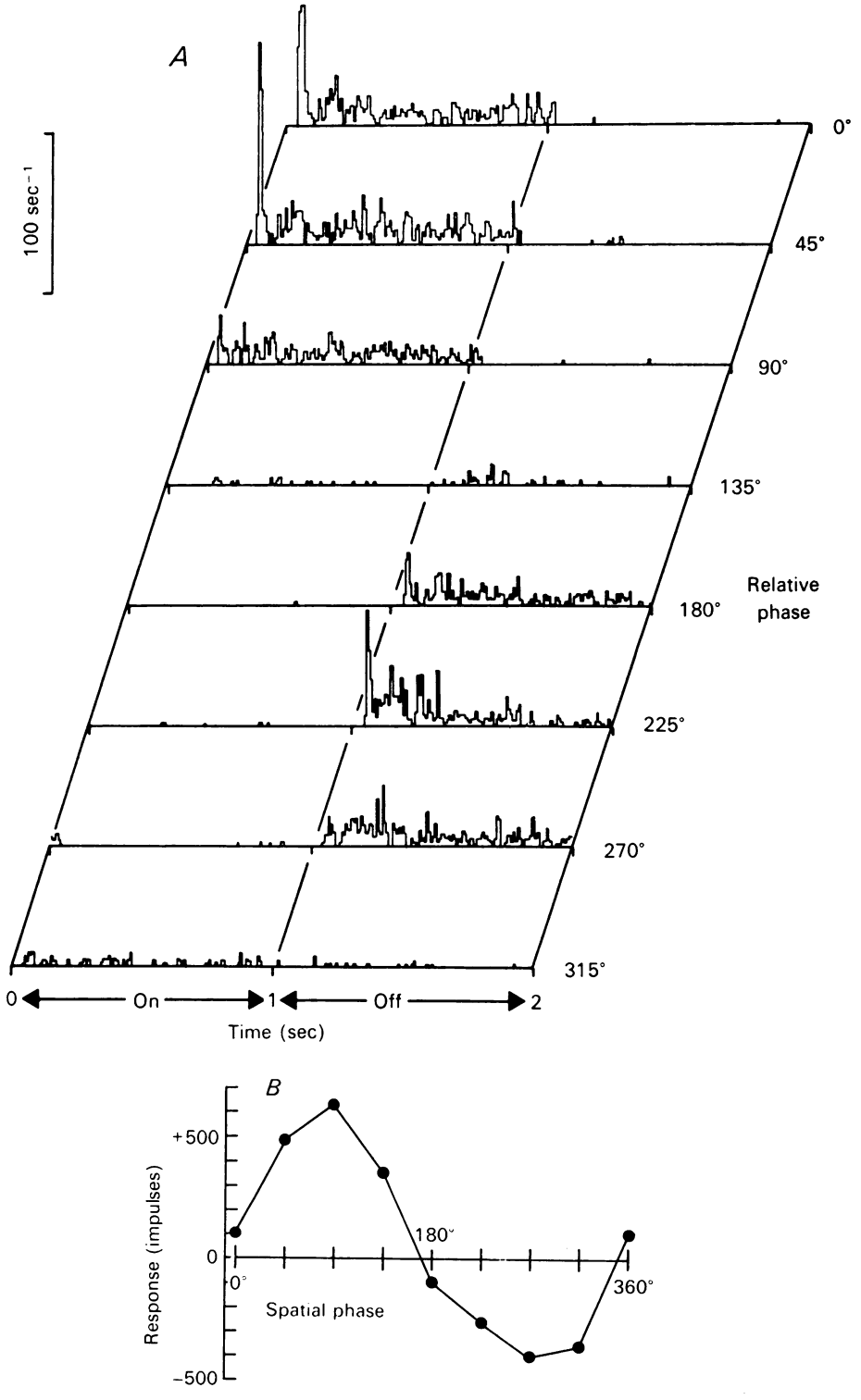

Fig. 3. For legend see facing page.

frequency, the modulated response component dominated, despite the fact that the response occupied more than half the cycle.

We do not have sufficient data to determine whether the degree of modulation in simple cell response is bimodally distributed into linear and non-linear modes, or whether there is a continuum between the two. It is possible that the division of simple cells into linear and non-linear groups on the basis of their responses to moving gratings alone may be arbitrary, but the results of our tests using stationary gratings validate this classification.

Responses to stationary gratings

Enroth-Cugell & Robson (1966) examined the responses of retinal ganglion cells to stationary sinusoidal gratings, and used the results as an indication of the presence or absence of linear spatial summation. The amplitude and wave form of the response of these cells depends on the spatial phase (or position) at which the grating is presented.

In retinal X cells, which sum linearly, a spatial phase can be found at which the introduction and withdrawal of a grating elicits no response. Changing the phase of the grating in one direction results in an incremental response to its introduction; a shift in the other direction results in a decremental response. The wave form of the response to the introduction of the grating at one phase is the inverse of the response to its withdrawal, or of the response to the introduction of the grating at a phase 180° different. A plot of the magnitude of the neurone's response as a function of grating phase describes a sine wave that varies symmetrically about zero response; the two zero crossings of the sine wave represent the two 'null phases' for the neurone (Hochstein & Shapley, 1976*a*).

In retinal Y cells, which sum non-linearly, introduction and withdrawal of the grating elicits a response irrespective of spatial phase. This finding alone need not signify non-linear spatial summation (see Appendix); rather, the Y cell's non-linearity is shown by the fact that the response to the introduction of a grating is not the inverse of the response to its withdrawal. In fact, for a Y cell, there is always a phase at which the cell's responses to grating introduction and withdrawal are identical in form and amplitude (a pure 'on–off' response). Responses of this kind contain temporal frequencies that are not present in the stimulus, and may result from either a full-wave rectification, or the summed outputs of two half-wave rectifications of opposite sense (see Hochstein & Shapley, 1976*b*).

We examined the responses of simple cells to stationary gratings of different phases. In addition to the *flashed* mode of presentation used by Enroth-Cugell & Robson, in which a grating is periodically exchanged for a blank field of the same

Fig. 3. *A*, the responses of a simple cell to stationary sinusoidal gratings turned on and off at the spatial phases indicated beside each histogram. The spatial frequency of the gratings was 0·75 c/deg, they all had a contrast of 0·72, and were turned on for 1 sec every 2 sec. *B*, a graph showing the amplitudes of the responses of this neurone as a function of spatial phase. Positive-valued responses are those that accompanied the presence of the grating, negative-valued responses are those that occurred in its absence. The ordinate represents the total number of impulses elicited by fifty presentations of each grating.

mean luminance, we used two *modulated* modes of presentation: square-wave and sine-wave modulation. A square-wave modulated grating is merely a grating whose contrast is multiplied in time by a square wave whose value is either +1 or −1; the grating is replaced instantaneously by a grating of opposite phase twice during each cycle; and it may be considered as a grating whose spatial phase shifts by 180° twice each stimulus cycle. A sine-wave modulated grating is a stationary grating multiplied in time by a sine wave whose amplitude varies between +1 and −1; its contrast varies continuously, and for half its cycle it is present in one spatial phase and for half it is present in the opposite phase. Any of these modes of presentation may be used to analyse the spatial summation behaviour of a visual neurone, so long as note is made of the temporal frequencies present in the stimulus and in the response, and the two compared for the presence of output frequencies absent from the input.

We examined twenty-five simple cells' responses to stationary gratings. Of these, 17 (68 %) appeared to show linear spatial summation; those that were linear on this test also appeared linear in their responses to moving gratings. Similarly, the remaining eight simple cells that appeared non-linear in their responses to stationary gratings also appeared non-linear in their responses to moving gratings.

We encountered two different varieties of linear simple cell, and the responses of the most common and simplest of these varieties are exemplified by those shown in Fig. 3*A*. At two spatial phases 180° apart there was little or no response to either the introduction or withdrawal of the stimulus. At the two phases 90° from these 'null' phases, the response was greatest: in one case (45°) there was an incremental response to the grating's introduction; in the other (225°), there was a similar incremental response to the grating's withdrawal. In the absence of significant resting discharge, we could not directly compare responses to introduction and withdrawal of the same grating. Nevertheless, it may be seen that the portions of the response to any grating that are visible above the threshold (zero) firing level are closely mirrored by the visible portions of responses to a grating of opposite phase. In particular, there is no suggestion that the response wave forms contain any energy at the even harmonic frequencies absent from the stimulus wave form.

Fig. 3*B* shows a graph of this neurone's response amplitude as a function of spatial phase. Excitatory responses to grating removal are plotted as negative values, since we assume that they accompany an unseen hyperpolarization of the membrane at the grating's introduction. The nearly sinusoidal variation in response amplitude with phase, and presence of two phases 180° apart at which no response was elicited, are reminiscent of the behaviour of X cells in the retina and lateral geniculate nucleus (Enroth-Cugell & Robson, 1966; Hochstein & Shapley, 1976*a*; Shapley & Hochstein, 1975). Thirteen simple cells behaved in this way, and acted as though they summed influences linearly from all parts of ther receptive fields. That there exists a pair of phases at which a flashing grating elicits no response suggests that all of the more peripheral neural elements of the visual system that influence such a neurone give responses whose amplitude is proportional to grating contrast, and that the responses of these elements to a luminance increment are the precise inverse of their responses to luminance decrement (see Enroth-Cugell & Robson, 1966).

In four cells, we observed a more complicated form of linear behaviour. Fig. 4*A* shows the responses of one such cell to square-wave and sine-wave modulated

gratings at different spatial phases; it is apparent that there was a response at each spatial phase for both these modes of presentation. As we show in detail in the Appendix, this need not indicate non-linear spatial summation. Note that the response to the first phase shift in the square-wave modulation cycle was not the same as the response to the second shift. In fact, for each point in the response to the first phase shift where there was excitation, there seems to be inhibition (suggested by a silent period in the record) in the response to the second phase shift. It is possible, then, that the cell gave inverse responses to grating introduction at opposite phases, behaviour characteristic of a linear neurone. Closer examination of the response wave forms elicited by the square-wave modulation reveals several components: a brief initial transient, followed by one or two slower responses (these components may be most clearly seen in the record for a phase of 0°). Furthermore, the amplitudes of these components appear to vary independently with spatial phase: the brief transient is most obvious at 0°, the second component most obvious at 67·5°, and the third component most obvious 157·5°. Although there are phases at which one or the other of these components appears to have zero amplitude, there is no phase at which they are all zero, and at which the neurone does not respond.

The four simple cells that behaved in this manner had odd-symmetric receptive fields; in the Appendix, we show that behaviour of this kind could be obtained from a linearly summating simple cell only if its receptive field contains two or more spatially offset regions that differ in their temporal response properties. Each region will have a spatial phase at which it gives no response, but since the regions are spatially offset from one another, these phases may be different for each region. Since the responses elicited from the different regions occur at different times following the stimulus, they will never cancel one another to give a null.

In the Appendix, we demonstrate that a linear neurone of this kind should respond in a rather special way to gratings of different phases when their contrasts are *sinusoidally* modulated in time. The response must, of course, contain only the temporal frequency of modulation (neglecting a rectification if that is present). Whereas for a retinal X cell or a linear simple cell of the kind shown in Fig. 3, this response would vary in amplitude but not in phase as spatial phase is varied, the responses of the more complicated variety of linear cell should vary in phase and also possibly in amplitude as spatial phase is varied. Moreover, a polar plot of response amplitude and response phase should describe an ellipse centred on the origin.

Fig. 4*A* (right-hand side) shows the responses of this neurone to sinusoidally modulated gratings: the temporal phase of the response does, indeed, vary as a function of grating spatial phase. Moreover, the polar diagram of response amplitude and response phase shown in Fig. 4*B* (filled symbols) resembles an ellipse apart from a slight wasp waist. This wasp waist could be explained if this neurone's maintained discharge level was not zero, but effectively *negative* (the resting level of transmembrane potential was somewhat *below* the threshold necessary to trigger an impulse). This negative maintained discharge would have the effect of causing us to underestimate the amplitude of small responses more than the amplitude of large ones; if we correct the data for an assumed negative discharge rate of −8 'spikes per second', the data (plotted in Fig. 4*B* as open symbols) now give a near-perfect ellipse.

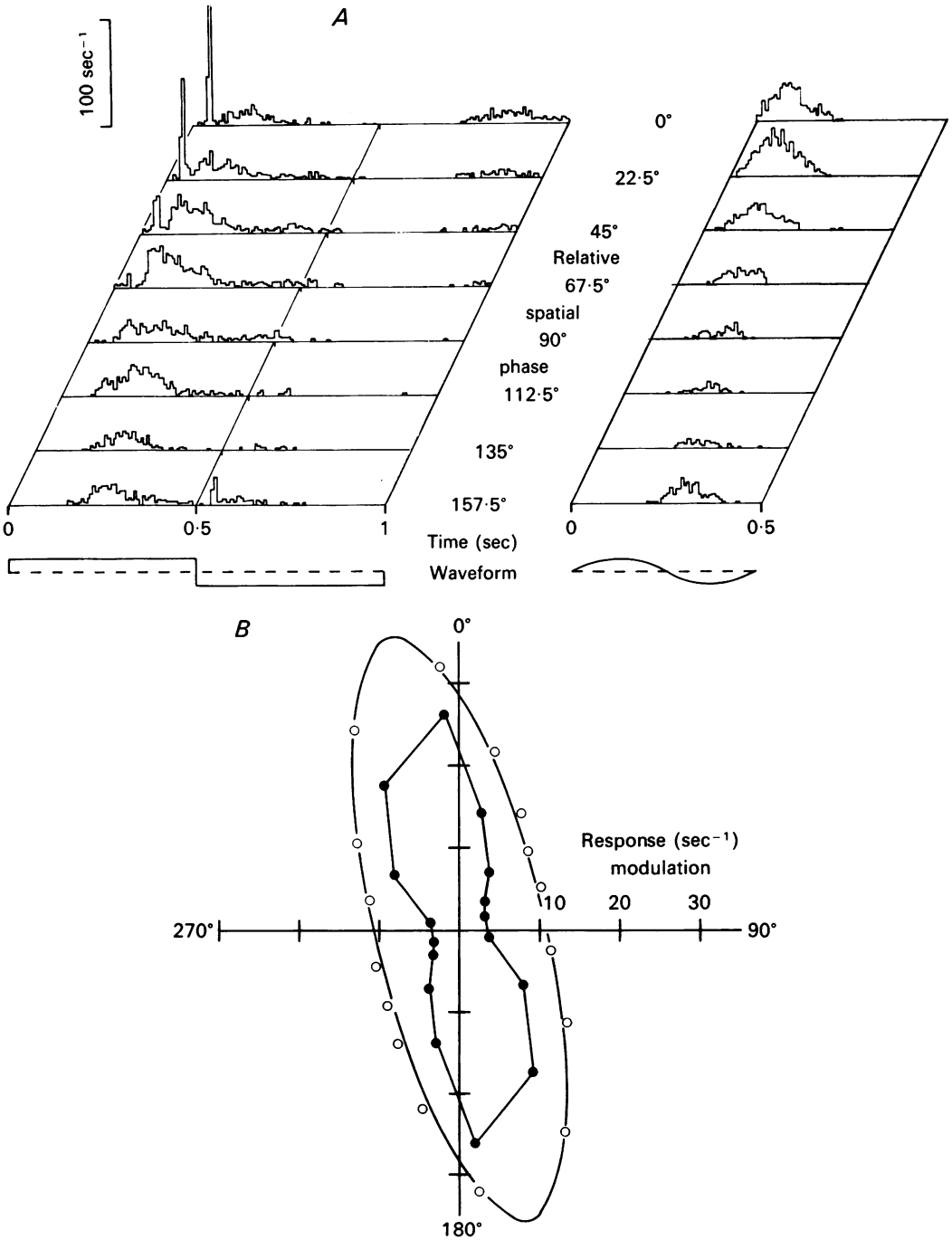

Fig. 4. *A*, the responses of a simple cell to stationary sinusoidal gratings modulated in time with either a square wave at 1 Hz (left) or a sine wave at 2 Hz (right), at the spatial phases indicated. The spatial frequency of the gratings was 0·5 c/deg, and they all had a contrast of 0·5. *B*, a polar diagram showing this neurone's responses to sine-wave modulated gratings of different spatial phases (data from the records shown in *A*). The amplitude of the fundamental component of the response is represented radially, while the angular coordinate indicates the temporal phase of each response. The filled symbols represent the unaltered data from the experiment; the open symbols and the ellipse fitted to them represent the same data corrected for a maintained firing rate of −8 'spikes per second'; the neurone had no maintained discharge in the absence of stimulation.

The orientation and eccentricity of the ellipse depend on several factors, including the temporal phase difference between the different response components, and the spatial offset between the different receptive field regions. By estimating the spatial offset between regions from our receptive field map for this cell, and assuming the existence of only two regions, we have calculated the latency difference between the two regions as being roughly 25 msec, with the delay of the more rapid response being roughly 40 msec at this temporal frequency (2 Hz).

Eight simple cells (32 % of the ones that we tested in this way) gave responses to stationary grating that could only be interpreted to indicate that they showed significantly non-linear spatial summation. The responses of one of these cells to moving gratings are illustrated in Fig. 1*B*, and the responses of this neurone to square-wave modulated gratings of different spatial phases are illustrated in Fig. 5*A*. The response of this neurone resembles in part the response of the linear simple cell shown in Fig. 3. For example, at a phase of 45°, the response appears as though the cell might be linear. There are, however, several phases at which the introduction of a grating and its shift by 180° elicit similar responses (e.g. 112·5°). These responses reflect the appearance of energy at the even harmonics of the stimulus' temporal frequency; these frequencies are absent from the stimulus square-wave, which is composed, of course, entirely of odd harmonics. These results are plotted as a function of spatial phase in Fig. 5*B* which shows that the introduction of a grating over a range of phases of about 270° elicited a significant response from this neurone. Similar data plotted for the linear simple cell in Fig. 3*B* show that the cell gave excitatory responses over a range of 180° – the positive-going half-cycle of a sine wave. The behaviour of the non-linear neurone is, in this respect as in its responses to moving gratings (Fig. 1*B*), reminiscent of the behaviour of retinal Y cells (Enroth-Cugell & Robson, 1966; Hochstein & Shapley, 1976*a*).

Comparison of receptive fields with grating responses

Our discussion has thus far confined itself to a description and analysis of the responses of simple cells to grating stimuli. In this part of the paper we turn to the question of the relationship between a neurone's response to gratings and its receptive field structure, defined with conventional geometric stimuli. Hubel & Wiesel's description of simple cell receptive field properties suggested that the configuration of effective stimuli for these cells could be predicted from their receptive field maps determined with stationary stimuli; complex cells, on the other hand, were described as having stimulus preferences that were not simply related to their receptive field maps.

Qualitative comparisons

An effective qualitative comparison may be made by simply assuming that the most effective grating stimulus for a neurone will be of such a spatial frequency that one bar of the grating just fills the most sensitive region of the neurone's receptive field. The bars of a coarser grating would always fall in such a way that some of the light (or darkness) they present would fall outside this region, and a finer grating would always fall in such a way that more than one bar of the grating would be present within the region. In our initial receptive field maps of simple cells, we were

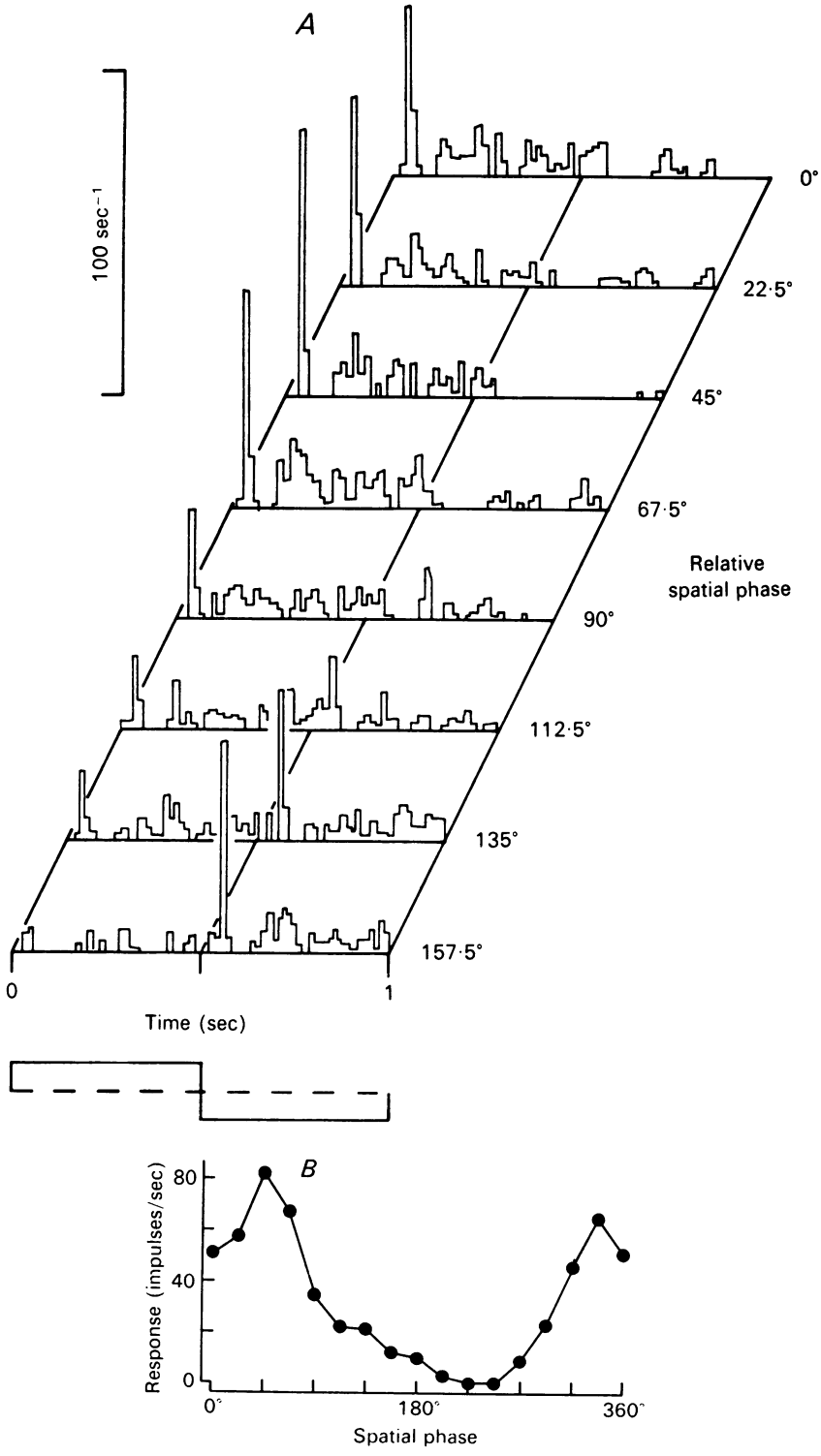

Fig. 5. For legend see facing page.

particularly careful to map out the extent of the different regions present in the cells' receptive fields.

Fig. 6 presents data comparing the size of the most sensitive region of a simple cell's receptive field with that neurone's optimum spatial frequency. The abscissa is the ratio of observed and expected values for the size of this region, where the expected value was taken as one half the period (or the width of one bar) of the optimum-frequency grating; there was quite reasonable agreement between observation and prediction. The mean ratio for this type of cell was 1·02 (S.D. 0·37), showing that, on average, one bar of the optimum grating just filled the most sensitive region of a simple cell's receptive field. We did not find any difference in this respect between simple cells classed as showing linear (n = 32, mean = 0·99) or non-linear (n = 15, mean = 1·04) spatial summation on the test outlined above.

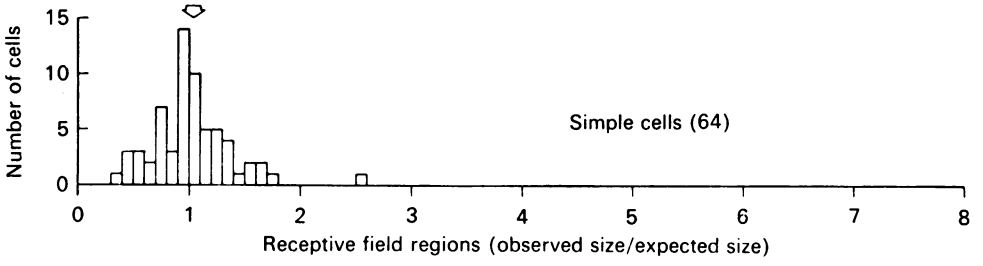

Fig. 6. A comparison of the receptive fields of sixty-four simple cells with their preferences for the spatial frequency of sinusoidal gratings. The abscissa plots the ratio of the width of the most sensitive region of each neurone's receptive field, measured during qualitative receptive field mapping, and the width of a single bar of a grating of the spatial frequency to which the neurone was most sensitive. The receptive field region whose width was used to calculate this ratio was the one that gave the most vigorous response to stationary bars.

Quantitative comparisons

One of the reasons that we chose to use sinusoidal gratings in our experiments is that they permit us to use the techniques of Fourier analysis to compare a neurone's receptive field structure with its stimulus specificity. Any wave form may be decomposed by Fourier transformation into a unique set of sine waves of different amplitude, frequency and phase; conversely, inverse transformation of a set of such

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Fig. 5. *A*, the responses of a simple cell to stationary sinusoidal gratings modulated in time with a 1 Hz square wave at the spatial phases indicated. The spatial frequency of the gratings was 0·75 c/deg, and they all had a contrast of 0·5. *B*, a graph showing the amplitudes of the responses of this neurone as a function of spatial phase. Responses that accompanied the introduction of a grating are plotted; for phase values between 0° and 157·5°, these responses are shown in the first half of each histogram of part *A*; for higher phase values, the responses are shown in the second half of each histogram in part *A*. As there was no period during the experiment when the grating was absent from the screen, no negative values are represented; the graph corresponds to, and should be compared with, only the positive-valued points in Fig. 4*B*. The response amplitude plotted is the average peak firing rate elicited during the brief transient burst of firing about 100 msec after the introduction of the grating.

sine waves yields a particular wave form. For a linear system, the Fourier transform of its *frequency response* measured with sine waves is its *impulse response*, the response it gives to a unit impulse. For a visual neurone when we are dealing with the domain of space we wish to compare the *spatial* frequency response with the *spatial* impulse response. We made extensive measurements of the sensitivity of striate neurones to sinusoidal gratings of different spatial frequency, giving us the first of these data sets (Movshon *et al.* 1978*b*). The other, which we will term the *line-weighting function*, is a map of the neurone's receptive field obtained with thin lines (spatial impulses) presented at different positions across the receptive field. For a linear neurone these two measures should be related by Fourier transformation.

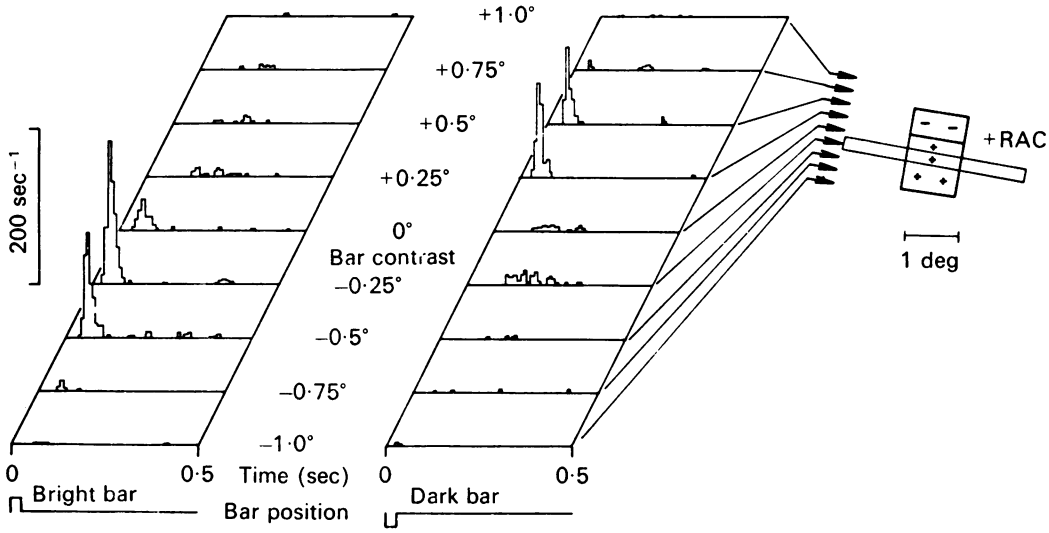

Fig. 7. An experiment to determine the line-weighting function of a simple cell classified as having linear spatial summation. A diagram of the neurone's receptive field is shown at the upper right, along with the position of the *area centralis* (+). A bar of the width used in the experiment is superimposed on the receptive field diagram; the length of all bars was 10°. The arrows indicate the nine bar positions tested; each position was separated from its neighbours by one bar-width (0·25°). Each stimulus was briefly flashed on to the receptive field for 64 msec, once every 500 msec.

Line-weighting functions were determined for twenty-eight simple cells. We always made these measurements with thin stationary bars of box-car luminance profile, whose width was chosen to be between one eighth and one sixteenth the width of the receptive field under study. The positions at which these bars were presented were separated by the width of each bar, so that the positions were precisely adjacent and non-overlapping. Since we measured contrast *thresholds* for sinusoidal gratings, we initially planned to obtain similar sensitivity measurements for thin lines. In view of the low sensitivity most striate neurones have for thin stationary lines, we instead compiled averaged response histograms of neuronal responses to these stimuli. We used bars whose luminance was brighter or darker than the 150 cd/m^2 background by 75 or 150 cd/m^2; these contrast levels were within the range of linear response in most cases and any distortion of the form of the line-weighting function that resulted

was minimal. We used bars that were either flashed on and off or square-wave modulated in all cases. For most complex cells and some simple cells, we mapped the receptive field with briefly flashed (16–64 msec) lines of both polarities (bright and dark). Simple cells were often relatively unresponsive to these brief stimuli, and when necessary we used long flashes (typically 500 msec on, 500 msec off) or square-wave modulation (bright bar present for half the cycle, dark bar present in the same position for the other half cycle) to obtain these data; there were no important differences between line-weighting data obtained with stimuli of different durations.

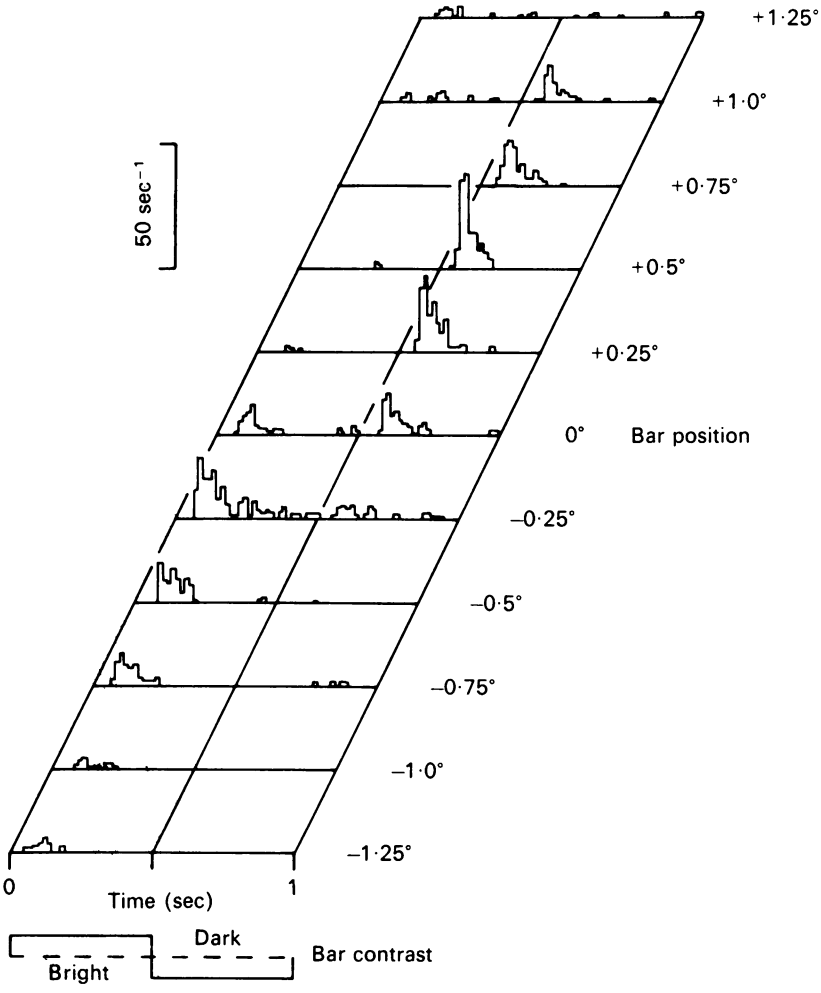

Fig. 8. An experiment to determine the line weighting function of a simple cell classified as having non-linear spatial summation, obtained using bars whose contrast was square-wave modulated at 1 Hz. For the first half of each record, the bar was bright, for the second half, it was dark.

Fig. 7 shows the responses of a typical simple cell to thin lines of both polarities briefly flashed on its receptive field. The experimental situation is diagrammed at the upper right, showing the location (with respect to the right *area centralis:* RAC)

and *map of neurone's* receptive field. One of the lines used in this experiment is superimposed to scale on the diagram (in width; its length was 10°), and the nine positions used are indicated by arrows.

This neurone's responses at any position could be interpreted as showing inversion when stimulus polarity was inverted, neglecting an obvious rectification. Thus at a position of −0·25° a bright bar elicited a vigorous response lasting until roughly 100 msec after stimulus onset; a dark bar elicited a smaller response, which did not commence until after this time. A similar situation obtained in reverse for bars at a position of +0·25°. This behaviour is compatible with the hypothesis that this neurone, like other simple cells showing linear spatial summation, was acting as a linearly summating device with rectification at its output.

Fig. 8 illustrates the responses of a simple cell, classified as showing non-linear spatial summation on the basis of previous tests, to square-wave modulated bars presented in different positions across its receptive field. At most positions, this neurone responded with a brief discharge to the onset of either the bright-bar or dark-bar portions of the stimulus cycle. For these positions, we could, in view of the absence of maintained activity, view the responses to bright and dark bars as being the inverse of one another. However, at two positions in its receptive field (0° and −0·25°), the neurone gave excitatory responses to both bright-bar onset and dark-bar onset: 'on–off' responses. These responses could not be interpreted as resulting from a linear underlying process. The identity of this neurone as a simple cell was not in doubt, however: it clearly gave larger responses to larger bars confined to one or the other of its receptive field regions, and reduced responses to a bar that invaded both regions.

Comparison of line-weighting functions with spatial frequency tuning. For those neurones for which we had obtained both line-weighting and spatial frequency tuning data, we were able to compare the two data sets via Fourier analysis. For several reasons, however, this procedure could not be strictly rigorous. First, our spatial frequency tuning data were based on sensitivity measurements while the line-weighting functions were based on response measurements. This does not greatly affect the results since response and sensitivity measurements of spatial tuning are similar (Movshon *et al.* 1978*b*). However, the units of measurement differed, so the line-weighting functions and inverse transforms were normalized to a value of 1·0 at their respective maxima. Secondly, to execute a Fourier transform, the amplitude and *phase* of the response at each spatial frequency must be known. Phase information was lost in our procedure for determining contrast sensitivity. We therefore assumed that the receptive fields were either perfectly even-symmetric or perfectly odd-symmetric. Third, spatial frequency tuning was determined with moving gratings while line-weighting functions were obtained with stationary lines. These problems are not negligible, but we feel that they did not greatly affect our data because of the satisfactory results obtained from simple cells compared with the gross failures experienced with complex cells (Movshon *et al.* 1978*a*).

Fig. 9 shows the results of this comparison for four simple cells. In each case, the histogram represents the normalised line-weighting function, and the width and position of its bars represent the width and position of the bars used in testing; positive responses represent incremental responses to bright stimuli; negative responses represent incremental responses to dark stimuli. In *A*, where the histogram is double-valued at some positions, the neurone gave responses to both bright and dark bars that were identical in time course at that position; neurones for which this was true were always classified as having non-linear spatial summation on the

basis of their responses to gratings. The solid lines superimposed on the line-weighting histograms represent the predicted line-weighting functions derived by Fourier transformation of the neurones' spatial frequency tuning curves; these tuning curves are inset beside each line-weighting histogram.

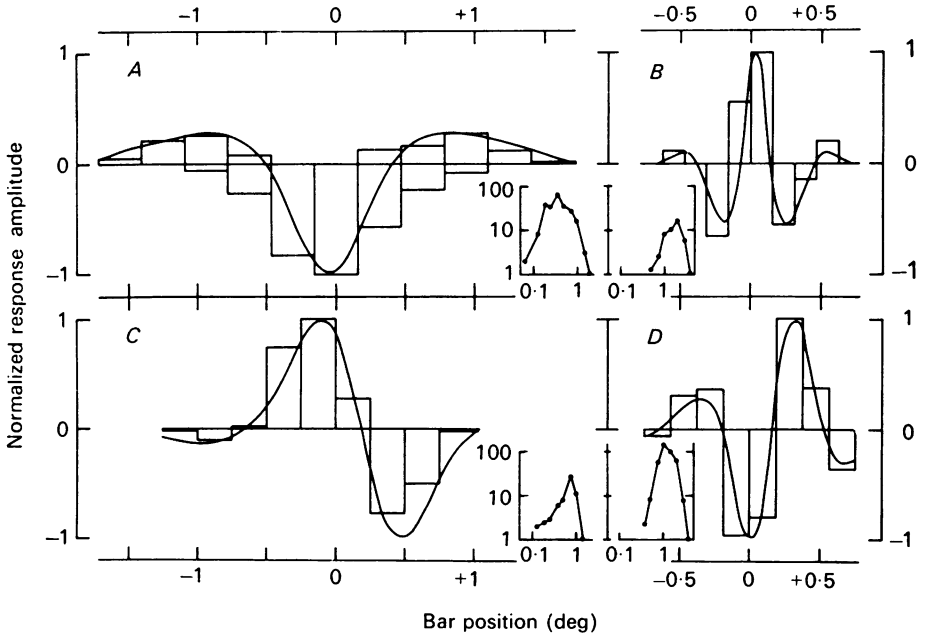

Fig. 9. A comparison between the observed line-weighting functions of four simple cells and the line-weighting functions predicted by inverse Fourier transformation of their spatial frequency tuning curves. Each cell's maintained discharge has been subtracted from its responses, and both the observed and predicted line-weighting functions have been normalized. Positive values in each line-weighting histogram represent incremental responses to the introduction of a *bright* bar; negative values represent incremental responses to the introduction of a *dark* bar. The width and position of the histogram bars indicate the width and position of the bars used in testing. The continuous curves represent inverse Fourier transforms of the cells' spatial frequency tuning curves. Even (*A*, *B*) or odd (*C*, *D*) symmetric transforms were selected to match observed line-weighting functions; they have been translated sideways arbitrarily to provide the best fit to these data. The spatial frequency tuning curve used to compute the predicted line-weighting function for each neurone is inset beside each diagram. The abscissa of these insets is spatial frequency in cycles per degree; the ordinate is contrast sensitivity, the inverse of the threshold contrast value for each spatial frequency.

Note that for some bar positions, the line-weighting function of cell *A* was double valued. This cell was classified as showing non-linear spatial summation on the basis of its responses to gratings, and gave incremental responses to the onset of bars of both polarities at the positions that are double valued (see Fig. 8). All the other neurones were classified as showing linear spatial summation, and gave incremental responses to *either* bright or dark bars at each position, but never to *both* (see Fig. 7).

It is clear that the agreement between observed and predicted line-weighting functions for these neurones was excellent, whether or not they showed linear spatial summation. One feature of these results is particularly interesting. When the neurone's

spatial frequency bandwidth was narrow, the predicted line-weighting functions exhibited additional 'ripples', regions antagonistic to the adjacent one. In every case that our measurements of line-weighting extended far enough, the neurone's responses reflected these additional regions (e.g. Fig. 9*B*, *D*). These regions were usually very weak and nearly impossible to detect without averaging responses, but were never absent from our line-weighting measurements when their appearance was predicted.

These results confirm our hypothesis that simple cells may act linearly in summing influences across space, since this agreement between spatial tuning and line-weighting is characteristic of a linear neurone. It is interesting that the agreement was good for those simple cells that showed non-linearities of spatial summation; it is clear that those non-linearities are not of such a type as to make a linear approximation to the neurones' behaviour impossible.

DISCUSSION

Linearity of operation in simple cells

We have shown that under certain conditions, simple cells in the striate cortex may act as linear spatial analysers, whose visual responses may be described as resulting from perfect summation across the receptive field. The extent to which this linear range of operation holds is limited, however, and we should consider the nature of known and probable non-linearities.

First, we have made the assumption that the rectified output of simple cells reflects nothing more than a threshold non-linearity of output processing. We have assumed that during silent periods in a neurone's responses, a particular wave form is being followed by the neurone's transmembrane current, even though we cannot observe this wave form. Although we have observed no behaviour in linear simple cells to suggest that this assumption is misplaced, we should note that the rectification might conceal a multiplicity of non-linear evils. It may be possible to use pharmacological and visual techniques to elevate simple cells' maintained discharge artificially, thereby altering the threshold level, in order to search for any such non-linearities.

Secondly, our analysis has been confined to stimuli presented at simple cells' optimum orientations and, when these cells showed a direction preference, presented moving only in the optimum direction. There is considerable evidence that intracortical inhibitory processes modulate the responses of simple cells, and that these processes are to some degree responsible for those neurones' orientational and directional selectivity (Bishop, Coombs & Henry, 1971, 1973; Blakemore & Tobin, 1972; Creutzfeldt, Kuhnt & Benevento, 1974; Sillito, 1975; Goodwin, Henry & Bishop, 1975). We may reasonably expect this intracortical inhibition to be non-linear in its effect and it is thus likely that simple cells will show increasing evidence of non-linear operation for stimuli that are increasingly different from optimum. We have some evidence that this is the case for direction selectivity, since the mean firing rate of simple cells can be decreased by grating stimuli moving in their non-preferred directions. Some of our data on spatial frequency tuning and responses to gratings suggests that it might also be the case for spatial frequency (Fig. 1; Movshon *et al.* 1978*b* and unpublished observations). Perhaps the most reasonable view of this

is that the intracortical inhibitory mechanisms act to increase simple cells' stimulus selectivity by attenuating responses to inappropriate stimuli; for appropriate stimuli, however, it is reasonable to view simple cells as essentially linear in operation. Since, when simple cells are active in the presence of stimuli that drive other cells much more effectively, it is unlikely that their signals will be much heeded, we may imagine that the function of inhibition is to decrease the response range of these neurones without affecting the linearly coded nature of their signals when their outputs are useful to the organism.

Non-linear simple cells. We were initially disturbed by the finding that a minority of simple cells acted in a non-linear manner. It is worth noting, however, that the magnitude of the non-linearities shown by these cells was always much less than that shown by complex cells (Movshon *et al.* 1978*a*). Although we have not studied this question in detail, it is possible that there is no fundamental difference in receptive field organization between linear and non-linear simple cells. The difference may in fact lie only in the levels of maintained activity in the geniculate neurones that provide their respective inputs: if simple cells act by adding the outputs of several sets of geniculate neurones, some on-centre and some off-centre, then even if those geniculate neurones sum linearly, the resulting output may show some non-linearity if the level of maintained discharge in the geniculate cells is low enough to allow some rectification. We might test this notion by performing our tests of linearity with stimuli of lower contrast, or in the presence of stimuli that would elevate the maintained discharge of geniculate neurones. It should in any case be borne in mind that non-linear simple cells, like linear ones, seem to respond to grating stimuli in a manner simply predictable from their receptive field arrangement, and thus provide an easily interpreted, if not linearly coded, output signal.

We may thus conclude that under certain conditions, a linear model of the simple cell's receptive field is satisfactory: simple cells can respond to visual stimuli in a manner suggesting that they simply integrate luminance over their receptive fields. This simple model is clearly unsatisfactory when applied to complex cells' receptive fields, and in the next paper we present an attempt to analyse the non-linear operations performed by these neurones.

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APPENDIX

The responses of linear neurones to temporally modulated gratings

A spatial sine wave grating whose contrast is being sinusoidally modulated in time may be represented by

$$L(x, t) = L_0(1 + C(\cos(2\pi f_t . t))(\cos(2\pi f_x(x + \phi)))),$$

where the value of $L(x, t)$ is the luminance of the grating at some position x degrees from an arbitrary origin along an axis orthogonal to its bars at time t, L_0 is the mean luminance, C is the contrast, f_t is the temporal frequency of contrast modulation, f_x is the spatial frequency in cycles per degree and ϕ is the spatial phase with respect to the origin. Simplifying by eliminating the terms relating to contrast and luminance, and by scaling x with f_x and t with f_t, we may represent this grating by

$$\cos(t).\cos(x + \phi).$$

Expansion of this expression yields

$$\cos(t).\cos(x).\cos(\phi) - \cos(t).\sin(x).\sin(\phi),$$

showing that the stimulus may be considered as two gratings separated by 90° in spatial phase presented at the same time. Changes in the value of ϕ will simply alter the relative amplitude of the two component gratings.

Consider a linear neurone whose receptive field contains two unitary regions that have different temporal characteristics. Let these two regions be spatially offset from one another, in that the value of spatial phase that optimally excites one of them is not the same as that for the other. Let the spatial phase of the stimulus be such that the region a is optimally excited for $\phi = 0$, and let there be no temporal phase shift in the response of region a (these assumptions are unimportant except that they simplify manipulation of the expressions). Let the sensitivity (or gain) of region a equal A. Region b is spatially offset from region a and will be optimally excited for $\phi = X$; since its temporal properties differ from those of region a, its response may have a temporal phase of T; its sensitivity is B.

The response of region a is

$$R(a) = A.\cos(\phi).\cos(t),$$

and the response of region b is

$$R(b) = B.\cos(\phi).\cos(X).\cos(t + T) - B.\sin(\phi).\sin(X).\cos(t + T),$$

where the two terms represent the response components due to the two component gratings of the stimulus. The neurone's response will equal $R(a) + R(b)$, given after expansion by

$$R = k_1.\cos(t) + k_2.\sin(t), \tag{1}$$

where

$$k_1 = A.\cos(\phi) + B.\cos(\phi).\cos(X).\cos(T) + B.\sin(\phi).\sin(X).\cos(T),$$

$$k_2 = B.\cos(\phi).\cos(X).\sin(T) + B.\sin(\phi).\sin(X).\sin(T).$$

The response will therefore be a sinusoid, of the same temporal frequency as the stimulus, with amplitude and temporal phase given by

$$(k_1^2 + k_2^2)^{1/2} \quad \text{(amplitude)},$$

$$\tan^{-1}(k_2/k_1) \quad \text{(phase)}.$$

The amplitude and temporal phase of the neurone's response will depend on ϕ (the spatial phase of the grating) to a degree determined by the values of X and T. A polar co-ordinate representation of response amplitude and response temporal phase determined for a full range of values of ϕ will have the form of an ellipse, centred on the origin, the lengths of whose major and minor axes are given by

$$R_{\text{maj}} = \left\{\frac{K+(K^2-4A^2B^2.\sin^2(X).\sin^2(T))^{\frac{1}{2}}}{2}\right\}^{\frac{1}{2}} \tag{2}$$

$$R_{\text{min}} = \left\{\frac{K-(K^2-4A^2B^2.\sin^2(X).\sin^2(T))^{\frac{1}{2}}}{2}\right\}^{\frac{1}{2}} \tag{3}$$

where

$$K = A^2+2AB.\cos(X).\cos(T)+B^2. \tag{4}$$

R_{maj} and R_{min} define the neurone's response amplitudes at the best and worst values of stimulus phase (ϕ), respectively. The eccentricity of the ellipse will vary as a function of A, B, X, and T from a circle to a single straight line, but will always be centred on the origin. R_{min} will equal zero, and the ellipse become a straight line *through* the origin, when any of A, B, X, and T equal zero. There will then exist two values of ϕ, 180° apart, at which no response is elicited, and the temporal phase of the response will be independent of ϕ save that it will shift by 180° when the value of ϕ passes through one of the nulls. If, however, all four variables are non-zero, a response will be obtained at all values of ϕ, and the temporal phase of the response will vary continuously with ϕ.

Enroth-Cugell & Robson (1966) described a class of cat retinal ganglion cells, X cells, which summate linearly. For every X cell, some spatial phase of a stationary, temporally modulating grating may be found that elicits no response; in our terminology, R_{min} equals zero. The receptive fields of retinal ganglion cells (and also of neurones in the lateral geniculate nucleus: Shapley & Hochstein, 1975) consist of two concentric regions, centre and surround. If we identify these regions with a and b above, since they are concentric, X will equal zero. Despite the fact that centre and surround may differ in their temporal properties, and the ganglion cell thus have a non-zero value of T, there will always be two 'null-positions' for a temporally modulated grating.

The receptive field configurations of simple cells in the striate cortex are more variable than those of retinal or geniculate cells (Hubel & Wiesel, 1962). The line-weighting functions of simple cell fields orthogonal to their receptive field axes often resemble those of ganglion cells, and have even symmetry: these cells have a central region flanked by two antagonistic regions. So long as these regions are of equal strength and have similar temporal properties, X may be considered equal to zero and a null position will be found if the neurone has linear spatial summation (Fig. 3). Other simple cells have receptive fields with odd symmetry, containing two side-by-side antagonistic regions of roughly equal strength; for these cells, X will not be equal to zero. If the temporal properties of the two regions are similar ($T = 0$), the cells will, if linear, have a null position. If, however, the temporal properties of the two regions differ, none of A, B, T and X will equal zero, and gratings of all spatial phases will elicit a response; the temporal phase of the response will vary continuously with spatial phase. We have observed this behaviour in several simple cells (e.g. Fig. 4),

all of which possessed receptive fields with odd symmetry. Similar behaviour was observed by Maffei & Fiorentini (1973, Fig. 6), and the receptive field they illustrate also had odd symmetry.

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