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RECEPTIVE FIELD ORGANIZATION OF COMPLEX CELLS IN THE CAT'S STRIATE CORTEX

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SUMMARY

1. All complex cells in the cat's striate cortex exhibit gross non-linearities of spatial summation when tested with sinusoidal grating stimuli. Their responses to *moving* gratings of all but the lowest spatial frequencies are usually dominated by a component that is not modulated by the passage of the bars of the grating across the receptive field. They give responses to temporally modulated *stationary* gratings that consist mostly of even harmonics of the stimulus frequency and that vary little in amplitude or wave form as the spatial phase of the grating is varied.

2. We compared complex cells' receptive fields with their sensitivity to sinusoidal gratings of different spatial frequencies. *Qualitatively*, the receptive fields are usually two to five times wider than the bars of the gratings that stimulate them most effectively. *Quantitatively*, the receptive field profiles of complex cells are invariably broader than those predicted by Fourier synthesis of their spatial frequency tuning curves, and in particular lack predicted spatially antagonistic regions.

3. We further examined the receptive field organization of these cells, using pairs of stationary lines flashed synchronously on their receptive fields. If both lines are of the *same polarity* (bright or dark), complex cells respond to the paired stimulus much less well than they do to either of its component bars, unless the bars are separated by less than about one quarter of the width of the receptive field. If the lines are of *opposite polarity*, one bright and one dark, the opposite situation obtains: closely spaced bars elicit small responses, while paired bars of larger separation are much more effective. In either case, the results are independent in general character of the *absolute* positions of the stimuli within the receptive field; rather, they depend in a manner characteristic of each cell on the *relative* positions of the two bars.

4. The two-line interaction profile that plots the change in a complex cell's response to one bar as a function of the position of a second added bar corresponds closely to the receptive field profile predicted from Fourier synthesis of the cell's spatial frequency tuning curve. These profiles may thus reveal the spatial characteristics of *subunits* within complex cell-receptive fields. We examined the nature of the interaction between these subunits by performing several two-line interaction experiments in which the onset of the second bar was delayed some time after the onset of the first. The results suggest that neighbouring subunits interact in a

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facilitatory fashion: for an interval after the presentation of one bar, responses to neighbouring bars are enhanced.

5. The subunits of a complex receptive field may, by their spatial properties, determine the spatial selectivities of complex cells, while the nature of the interaction among the subunits may determine these cells' sensitivity and selectivity for moving visual stimuli. Thus a model based on the properties of, and interactions among, spatially distributed subunits within complex cell receptive fields appears capable of explaining the visual response properties of these neurones.

INTRODUCTION

In the preceding paper (Movshon, Thompson & Tolhurst, 1978*a*) we demonstrated that, to a large extent, simple cells in the cat's striate cortex may be considered to sum locally linear light evoked influences across their receptive fields in a linear manner. In this paper, we turn our attention to the behaviour of complex cells.

Hubel & Wiesel (1962) defined complex cells as those neurones for which it was not possible to predict the optimum visual stimulus from a knowledge of the structure of the receptive field obtained with stationary stimuli. A complex cell typically responds with equal vigour to a thin line placed in a range of positions in its receptive field, yet responds poorly to a broader line in the same positions – a palpable failure of the principle of superposition, since the broad line may consist simply of the sum of a number of the (previously effective) thin lines, and yet elicit little or no response from the cell. Clearly, complex cells do not sum influences linearly from different parts of their receptive fields. The nature of the non-linearity has, however, received little attention since it was first described; nor has the receptive field of the complex cell been analytically treated in the literature.

Using techniques employed in the preceding paper, we first demonstrate that spatial summation in the receptive fields of complex cells is grossly non-linear. We then examine the nature of this non-linearity, and provide evidence that the complex cell receptive field is composed of a number of 'subunits' which interact in a complicated manner that results in the non-linearity of spatial summation. An informal model of the receptive field is then developed; this model appears capable of explaining the general response properties of complex cells.

METHODS

These were indentical to those detailed in the previous paper (Movshon *et al.* 1978*a*). Neurones were identified as being complex on the basis of their responses to hand-held stimuli, following the criteria of Hubel & Wiesel (1962). Usually the receptive fields could not be subdivided into separate inhibitory and excitatory regions. In a few instances, a subdivision could be made but, in contrast to simple cells, the width of these regions was noticeably greater than the width of the optimal spatial stimulus.

RESULTS

Of the 164 units recorded from the striate visual cortex of twenty-one cats, fifty complex cells were analysed quantitatively. We did not attempt to subdivide our population of complex cells. This should not be taken to imply that we believe them to be a homogeneous group (Hubel & Wiesel, 1962; Palmer & Rosenquist, 1974;

Cynader, Berman & Hein, 1976; Finlay, Schiller & Volman, 1976; Gilbert, 1977), but the observations and conclusions in the following pages apply to all complex cells we have examined; this may be due to the fact that our analysis was carried out using only elongated (10° long) stimuli optimally oriented for each receptive field, and many of the differences among different complex cells only become apparent when shorter stimuli of varying orientation are employed.

In the first part of this section, we describe the responses of complex cells to moving and stationary sinusoidal gratings to provide an initial description of the 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. Finally, we describe experiments that examine in detail the non-linearities of summation observed in complex cells, using stationary stimuli composed of pairs of bright and dark bars of variable spatial and temporal separation.

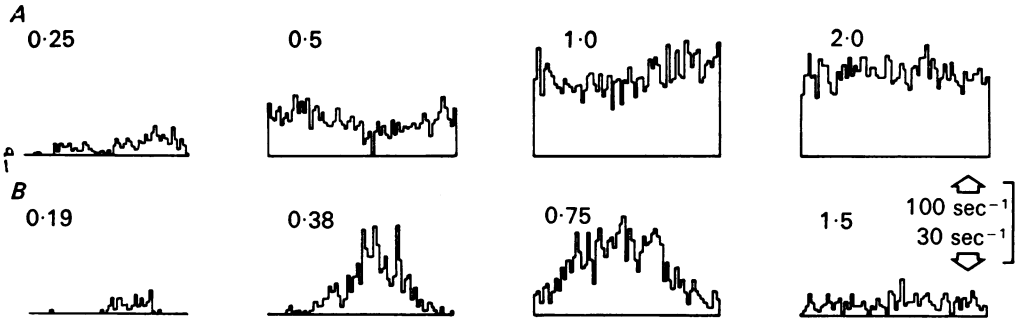

Fig. 1. The responses of two complex cells to sinusoidal gratings of different spatial frequencies, moving over their receptive fields at 2 Hz. Each histogram represents the average response of the neurone to the passage of one cycle of the grating across its receptive field; the number above each histogram 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. In this and the following Figures, each histogram is derived from 100 repetitions of the stimulus.

Responses to sinusoidal gratings

Wave form of response to moving gratings

The response of a linear neurone to a sinusoidal grating moving laterally at a constant velocity should take the form of a sinusoidal modulation of firing rate about the maintained discharge level. If the neurone lacks substantial maintained activity, the response may appear as a rectified sinusoid, the neurone being silent for part of the stimulus cycle. The response wave forms of complex cells stimulated with moving gratings could never be regarded as satisfying these criteria for linearity, although the departures from linearity varied in form and magnitude from cell to cell.

Fig. 1 illustrates the responses of two complex cells. For cell *A*, the response to gratings of all spatial frequencies consisted almost entirely of an unmodulated elevation of the firing rate; for cell *B*, responses to gratings of low spatial frequency were well modulated, but at higher frequencies, the response was almost totally

unmodulated. The non-linearity exhibited by cell *B* was similar in form to that shown by *Y* cells in the retina and lateral geniculate body (Enroth-Cugell & Robson, 1966; Shapley & Hochstein, 1975; Hochstein & Shapley, 1976*a*), and by non-linear simple cells in area 17 (Movshon *et al.* 1978*a*). The question then arises whether the non-linear simple cells are genuinely different from complex cells in this respect.

Fig. 2 plots the relative modulation (see Movshon *et al.* 1978*a*) present in the responses of the two complex cells shown in Fig. 1; for comparison, the data for one of the least-well modulated non-linear simple cells we encountered (cell *B* from Figs. 1 and 2 of the preceding paper) are included in the Figure. The complex cell

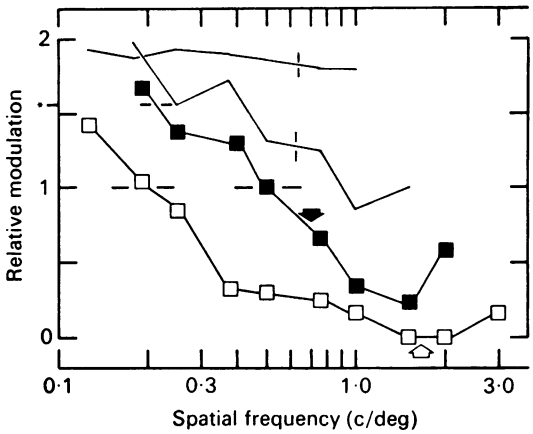

Fig. 2. Relative amplitudes of modulated and unmodulated components in the responses of three cortical neurones to moving gratings of different spatial frequencies. Relative modulation was determined by calculating the frequency components of the neurones' average responses by Fourier analysis, and then 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 complex cells whose responses are illustrated in Fig. 1 are shown; open symbols for the neurone of Fig. 1*A*, filled symbols for the neurone of Fig. 1*B*. The arrows indicate each neurone's optimum spatial frequency. The solid lines without symbols reproduce the data from two simple cells from Fig. 2 of the preceding paper (Movshon *et al.* 1978*a*).

with the less well modulated response (cell *A*) is represented by the open symbols and arrow; that with the more obviously modulated response (cell *B*) is represented by the filled symbols and arrow. For neither cell was the modulated response component dominant except at the lowest spatial frequencies; the f_0 (unmodulated) response component dominated both cells' responses to their respective optimum spatial frequencies. These results suggest that the responses of complex cells are more dominated by the unmodulated response component than are the responses of simple cells.

Responses to stationary gratings

In the previous paper (Movshon *et al.* 1978*a*) we demonstrated formally that a neurone that linearly sums light-evoked influences across its receptive field should

respond in a characteristic manner to stationary time-varying gratings as their spatial phase is varied. In general, while the temporal phase of the responses of such a neurone may vary in a complicated manner with spatial phase, the response to any one stimulus should contain only the temporal frequencies present in the stimulus (see Appendix to previous paper).

None of the twenty-three complex cells whose responses to stationary gratings were analysed could be considered to sum linearly. The non-linearity observed in these cells was similar to that shown by non-linear simple cells (Movshon *et al.* 1978*a*, Fig. 5), but was usually much more marked. While the responses of non-linear simple cells usually contained significant energy at the fundamental stimulus frequency, complex cell responses were nearly always dominated by second and higher even-harmonic response components. Thus the response of a complex cell to a sinusoidally modulated grating of almost any phase was usually a frequency-doubled sine wave without appreciable fundamental-frequency modulation; similarly, complex cell responses to square-wave modulated gratings were usually more or less pure 'on–off' responses.

Fig. 3*A* illustrates the responses of a complex cell as a function of spatial phase to square-wave modulated gratings of two spatial frequencies. At both spatial frequencies, introduction of the grating at any spatial phase elicited a brief response. At the lower frequency, the responses to two gratings 180° different in phase (the first and second parts of each record) were rarely identical; in other words, there was usually a significant fundamental frequency component in the response. At the higher spatial frequency, the responses to every phase were more-or-less identical, indicating that the contribution of the fundamental frequency component to the neurone's response was negligible. Fig. 3*B* plots these response amplitudes as a function of the spatial phase of the introduced grating for both spatial frequencies. At the lower spatial frequency, the amplitude of response depended much more strongly on spatial phase than it did at the higher spatial frequency. At neither spatial frequency was the phase dependence of the response as marked as it was for either the linear or non-linear type of simple cell (Movshon *et al.* 1978*a*).

It is noteworthy that complex cells' responses to moving gratings tended to be more strongly modulated at lower spatial frequencies, and that their responses to stationary gratings were more dependent on phase at lower spatial frequencies. Similarly, the degree of modulation in the responses of complex cells to moving gratings was always less than that in the responses of non-linear simple cells, and the phase-dependence of these simple cells' responses to stationary gratings was always less marked than it was in complex cells.

Comparison of receptive fields with grating responses

The remainder of this paper attempts to determine what aspects of receptive field structure determine a complex cell's stimulus preference.

Qualitative comparisons

If a neurone sums influences linearly across its receptive field, its stimulus preferences may be predicted from a knowledge of the spatial distribution of excitatory and inhibitory regions (Hubel & Wiesel, 1962). In particular, the optimum spatial frequency of sinusoidal gratings should be predictable from the size and distribution

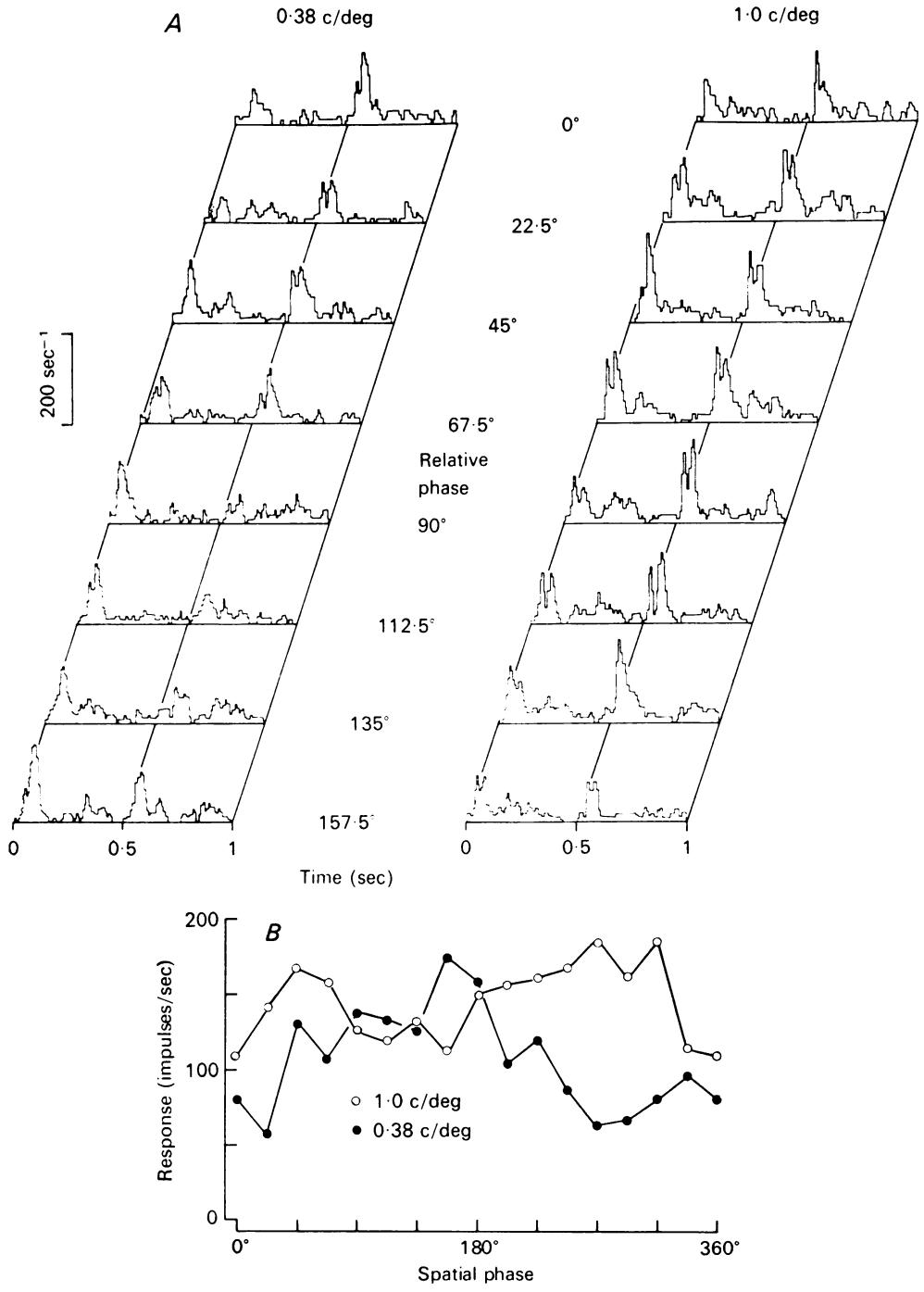

Fig. 3. *A*, the responses of a complex cell to stationary sinusoidal gratings modulated in time with a 1 Hz square wave at the spatial phases indicated. Two spatial frequencies were used in this experiment, and are indicated above each panel of histograms; all the gratings had a contrast of 0·5. *B*, the amplitudes of the responses of this neurone as a function of spatial phase for the two spatial frequencies tested. Responses to the introduction of each phase are plotted; points 180° apart correspond to the first and second peaks in the histograms of Fig. 3*A*. The amplitude plotted is the average peak firing rate elicited during the transient burst of firing after the introduction of each stimulus.

of these regions; this is the case for simple cells in area 17 (Movshon *et al.* 1978*a*). For most complex cells, we were able to map out one more-or-less homogeneous receptive field region with stationary stimuli; for some cells, we could not detect reliable flash-responses by ear, and we instead determined the 'minimum response field' (Barlow, Blakemore & Pettigrew, 1967) for this qualitative comparison.

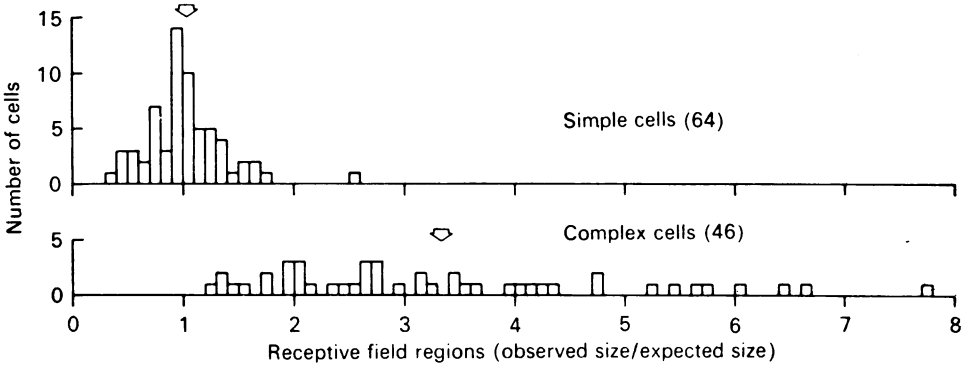

Fig. 4. A comparison of the receptive fields of sixty-four simple cells and forty-six complex cells with their preferences for the spatial frequency of sinusoidal gratings. The abscissa plots the ratio of the width of the most sensitive region of each neurone's receptive field, measured during qualitative receptive field mapping, and the width of a single bar of a grating of the spatial frequency to which the neurone was most sensitive. For most cells, the width of the whole receptive field was used, but for those complex cells with subdivided receptive fields, the width of the most responsive region was used.

The lower part of Fig. 4 presents data comparing the size of the most sensitive region of complex cells' receptive fields with the neurone's optimum spatial frequency (Movshon *et al.* 1978*b*). 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. It is quite clear that there is no simple relationship between receptive field size and optimum spatial frequency. In general, the observed receptive field sizes for complex cells were much larger than would have been expected on the basis of their spatial tuning characteristics. The mean ratio of 3·34 (S.D. 1·60) reveals that, on average, more than one and a half cycles of the optimum grating were present within the conventional receptive field of a complex cell. This should be compared with a ratio of 1·02 observed for simple cells (upper part of Figure). The ratios for complex cells were widely distributed (for several cells, more than three full grating cycles were present in the receptive field at optimum spatial frequency). This confirms Hubel & Wiesel's (1962) observation that the optimum stimulus width for a complex cell is less than the width of its receptive field.

Quantitative comparisons

Line-weighting functions were determined for twenty complex cells using thin stationary bright and dark bars of box-car luminance profile; the bars' width was chosen to be between one eighth and one sixteenth the width of the whole receptive field. The positions of the bars used in testing were adjacent and non-overlapping,

and they were usually briefly flashed on (16–64 msec). While the responses of some complex cells to flashed stimuli were inaudible in the irregular maintained discharge, averaging usually revealed brisk responses.

Fig. 5 shows the responses of a typical complex cell to thin lines of both polarities briefly flashed on to its receptive field. The experimental situation is indicated at the upper left, showing the location (with respect to the right *area centralis:* RAC) and approximate size of the neurone's minimum response 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. Inspection of the averaged

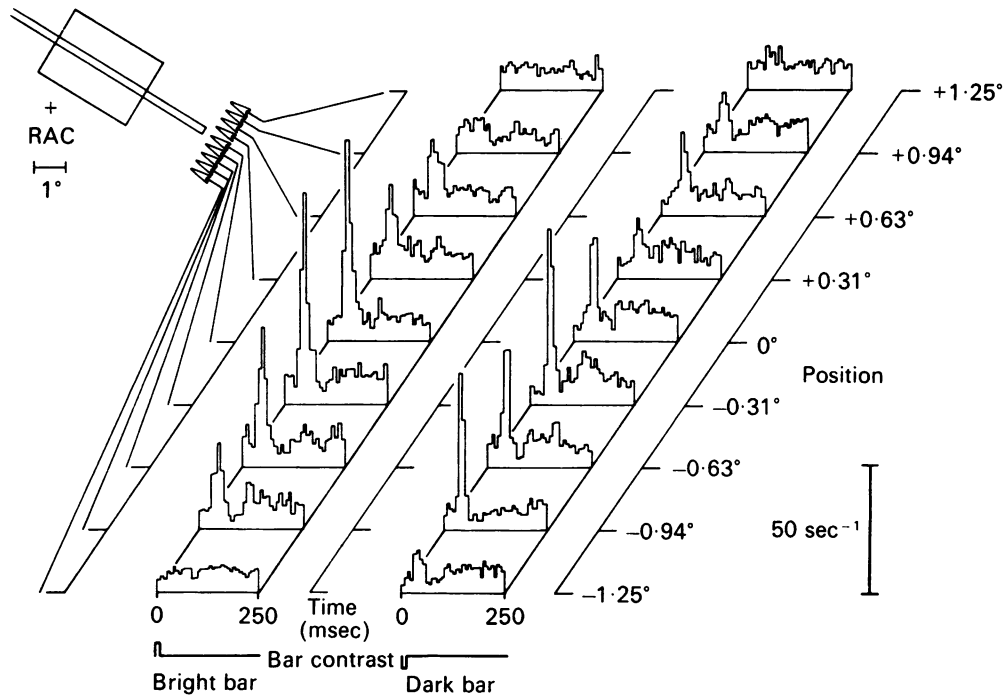

Fig. 5. An experiment to determine the line-weighting function of a complex cell. The minimum response field of the neurone is shown at the upper left, with the position of the right *area centralis* (RAC); a bar of the width used to obtain the line-weighting function is superimposed to scale on the receptive field; the bars in the experiment were all 10° long. The arrows indicate the nine bar positions tested; they were separated by the width of the bars (0·31°). Each stimulus was briefly flashed on for 32 msec every 250 msec, as indicated below each column of histograms.

response histograms shows that this neurone responded briefly to bright and dark lines presented at any position across the receptive field. The responses to lines of either polarity were similar in sign and time course, revealing a serious non-linearity of operation, since a linear neurone should give responses to increments and decrements that are the *inverse* of each other. Any position across the receptive field was more-or-less equally responsive to either bright or dark lines, although this was not always the case. Some complex cells gave responses predominantly to either bright or dark bars, while others gave better responses to bright bars in one part of the field

and better responses to dark bars in other parts (see below). Usually these regions were coextensive, as they were for the neurone in Fig. 5.

Comparison of line-weighting functions with spatial frequency tuning

For those neurones for which we had obtained both line-weighting functions and spatial frequency tuning data, we were able to compare the two sets of information using Fourier analysis; the methods involved were detailed in the preceding paper (Movshon *et al.* 1978*a*). Fig. 6 shows the result of such a comparison between predicted

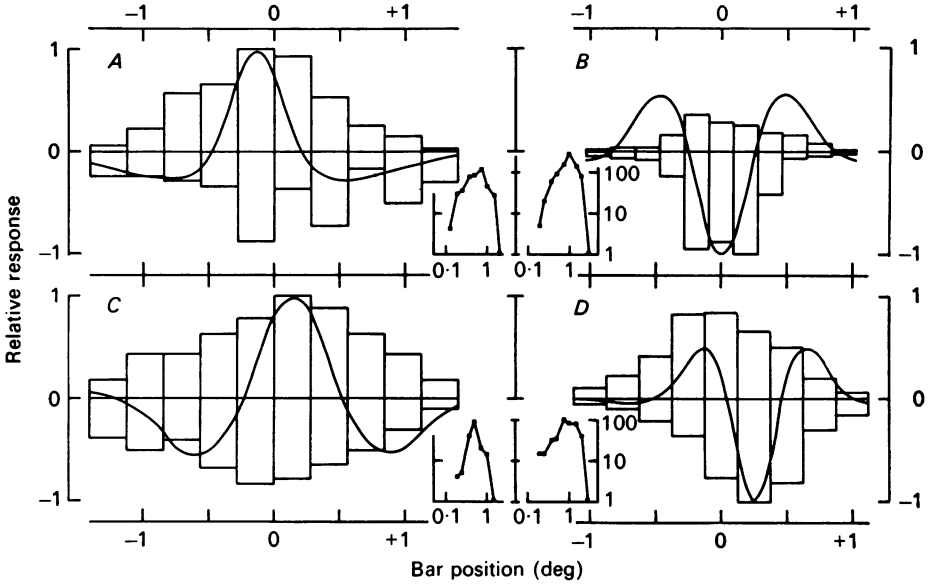

Fig. 6. A comparison between the observed line-weighting functions of four complex cells (histograms) and the line-weighting functions predicted from Fourier synthesis of their spatial frequency tuning curves (continuous curves).

Each neurone's maintained discharge has been subtracted from its responses, and both the observed and predicted line-weighting functions normalized to a peak value of 1. Positive values reflect incremental responses to bright bars, while negative values reflect incremental responses to dark bars; each histogram is double valued, since all these neurones gave responses to both bright and dark bars everywhere across their receptive fields (see Fig. 5).

The cells were not necessarily equally sensitive to both kinds of bars (e.g. cell *B*), nor were responses to the two kinds of bar always equally distributed across their receptive fields (e.g. cell *D*). The continuous curves represent even-symmetric Fourier transforms of the neurones' spatial frequency tuning curves; the spatial frequency tuning curve used to compute each prediction is inset in each part of the Figure; the abscissae of the insets are in cycles/deg, and the ordinates are constrast sensitivity (i.e. the inverse of the contrast at threshold).

and observed line-weighting functions for four complex cells. The line-weighting functions for all these neurones were double-valued throughout; they gave 'on–off' responses or responses to both bright and dark bars all across their receptive fields. It is clear that the line-weighting functions predicted for these neurones were very different from the ones that we observed. In each case, the predicted line-weighting function has a narrower central core than the observed function and possesses

inhibitory regions absent from the neurone's receptive field. In their spatial tuning, then, complex cells behave as though they are sampling the stimulus with a spatially restricted and spatially antagonistic weighting function within apparently homogeneous regions of their receptive fields. The nature of this antagonism and its origin are the subject of the final part of this paper.

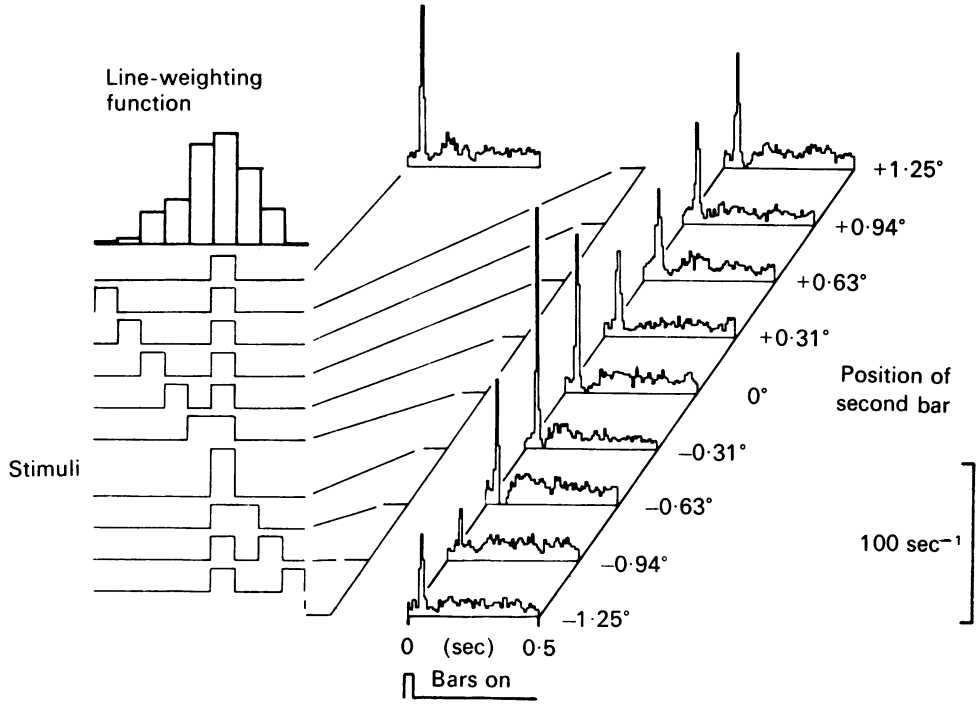

Fig. 7. An experiment to determine the two-line interaction profile of a complex cell, the same cell whose line-weighting function is illustrated in Fig. 5. The histogram at the upper left shows the response of this cell to bright bars at different positions across its receptive field, and is derived from the left-hand column of histograms in Fig. 5. Beneath it are drawn the luminance profiles of the stimuli used in the two-line interaction experiment. One bar was always presented at a position of −0·31°, and the cell's response to it alone is represented by the response histogram at the upper centre of the Figure. All other stimuli consisted of this bar and a second bar of the same width and contrast added at different positions across the receptive field, and the cell's responses to these line pairs are shown in the column of response histograms at the right. All the bars in this experiment were brighter than the background, and were flashed synchronously on to the receptive field for 64 msec every 500 msec as indicated by the trace at the bottom of the Figure.

The receptive field organization of complex cells

Responses to paired lines

The general experimental arrangement we used, and the results of a typical experiment, are illustrated in Fig. 7; the neurone is the one whose responses to single bars are illustrated in Fig. 5. The procedure was to repeat the line-weighting function with the difference that we also presented, simultaneously, a 'conditioning' bar at a fixed position in the receptive field. The histograms on the right of Fig. 7

show the response of the cell to pairs of bars occurring simultaneously but with varying spatial separation. Stimulus configuration is depicted on the left with the line-weighting function, i.e. responses in the absence of the conditioning bar, shown above, in register.

The response to the 'conditioning' bar alone is shown in the central histogram. Comparison of this histogram with those to the right reveals how the second bar, of

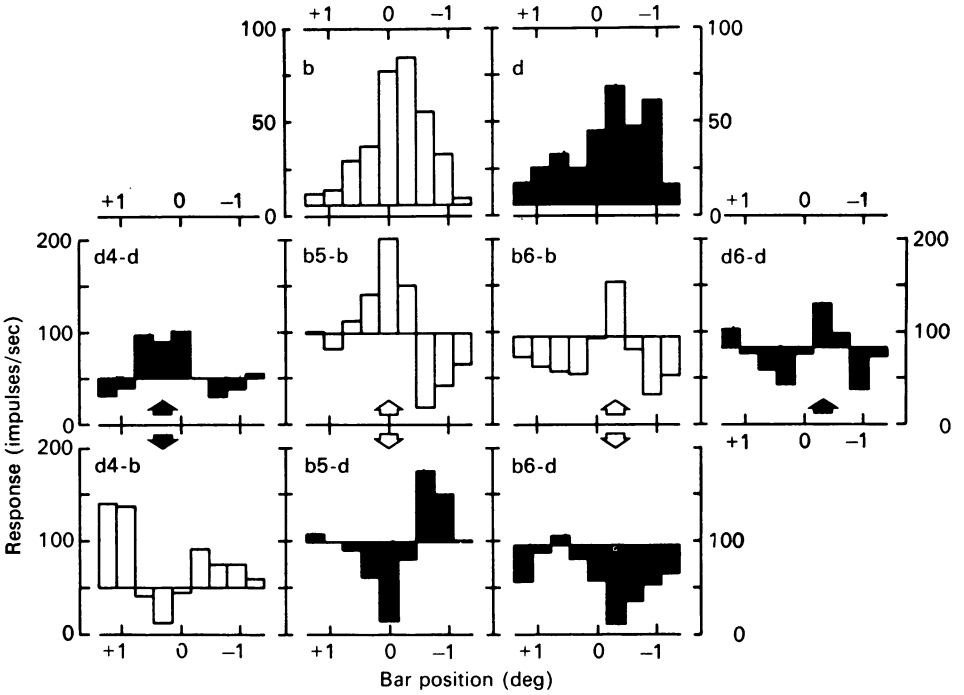

Fig. 8. The results of seven two-line interaction experiments performed on the complex cell whose responses are illustrated in Figs. 5 and 7. The two uppermost histograms represent the cell's line-weighting functions determined with bright (b) and dark (d) bars (Fig. 5); note the convention in this Figure that responses to bright testing bars are indicated by open histograms while responses to dark testing bars are indicated by filled histograms.

The second row of histograms represents the results of four two-line interaction experiments in which the two bars were of the same polarity. The arrows indicate the positions of the 'conditioning' bars in each experiment (open arrows for bright conditioning bars, filled arrows for dark ones), and the base line of each histogram represents the response elicited by each of the conditioning bars presented alone. Each histogram thus represents the *difference* in this response produced by adding a second bar at each position.

The bottom row of histograms represents the results of three two-line interaction experiments in which the bars were of opposite polarity. The conditioning bars in each case were the same as those used in the experiments represented by the superadjacent histogram in the middle row. Note that since the bright and dark bars were of equal contrast, the stimulus resulting from the exact superimposition of a bright conditioning bar and a dark test bar, or vice versa, was merely a blank field; thus the responses in the bottom row of histograms at the positions of the conditioning bars represent the neurone's maintained discharge.

The response measure in all cases is the average peak firing rate in the brief transient burst of firing following the introduction of each stimulus (see Figs. 5 and 7).

variable position, modified the response to the 'conditioning' bar. When the two bars were moderately separated, the neurone's response to the pair was considerably *less* than it was to the conditioning bar alone. Only when the bars were close together or actually superimposed (producing a single bar of doubled contrast) did the neurone respond as well or better to the pair of bars.

Thus pairs of bars presented within the receptive field show interactions which are not predictable from the line-weighting function for the neurone. The second bar, according to its position, can either summate with or antagonize the response to the fixed 'conditioning' bar. Two questions arise from this result. First, does the interaction depend on the *relative* or on the *absolute* positions of the two bars? Secondly, what would happen if the two bars were of different polarities: does the interaction depend on the 'sign' of the bars or just on their spatial location?

Seven separate two-line interaction experiments designed to investigate these questions are shown in Fig. 8. For comparison, we have included the line-weighting functions to both bright (b) and dark (d) bars for this neurone (upper two histograms; data shown in Fig. 5). In these and the remaining histograms the shading of the bins reflects the polarity of the testing bar (open = bright; filled = dark), irrespective of the polarity of any 'conditioning' bar.

The middle row of histograms show the effect of placing the 'conditioning' bar in four different positions, indicated by the arrows. Each bin represents the response to a pair of bars of a particular separation relative to the response to the 'conditioning' bar alone (which is shown as the base line of the histogram). Several features are clear from these data. First, the positions of maximum facilitation and maximum inhibition shift when the position of the conditioning bar is shifted. Facilitation was observed only for bars within 0·31° of the conditioning bar, and inhibition was strongest for bars 0·63° or more from the conditioning bar; thus the results were independent of the *absolute* positions of the two bars, but depended in a characteristic way on their *relative* positions. Secondly, similar two-line interaction profiles were obtained in conditions in which both bars were bright, or both bars were dark. Thirdly, when the 'conditioning' bar was placed to one side or the other of the centre of the receptive field, distant bars (more than 1·25° away) no longer inhibited the neurone's response to the conditioning bar; rather, there was slight facilitation at these positions (right-most bar in the histogram labelled d4-d; left-most bar in the histogram labelled d6-d). The results of the experiment illustrated in Fig. 7 are shown in the third histogram in this row (b6-b).

The bottom row of histograms illustrates the results of three experiments in which the polarities of the 'conditioning' and test bars were different. The 'conditioning' bar in each case was identical to that used in the experiment represented by the superadjacent histogram in the middle row, and the test bars were of inverse polarity, as indicated by the presence or absence of shading in the histograms. It may readily be seen in this situation that the two-line interaction profiles were inverted by making the two lines of opposite polarity. Wherever there had been facilitation of response for a pair of bars of the same polarity, there was now inhibition; conversely, wherever bars of the same polarity had inhibited one another, there was now facilitation. This behaviour was quite unpredictable from the neurone's line-weighting function: bright or dark bars presented alone elicited essentially identical responses from this neurone

at each position (see Fig. 5). Nevertheless, the interactions between different regions of the complex cell's receptive field were strongly dependent on the polarity of bar contrast, information that is not apparently available from the output of a complex cell tested with single stimuli. The precision with which this inversion could occur is most evident from a comparison of the second histograms of each of the two bottom rows (b5-b and b5-d).

We have obtained similar results from ten complex cells. In no case could the response of a complex cell to a pair of lines be simply interpreted as the sum of its responses to the individual lines; the interactions revealed were always of the form illustrated in Fig. 8, and the width of the interaction function was always less than the width of the single-line weighting function.

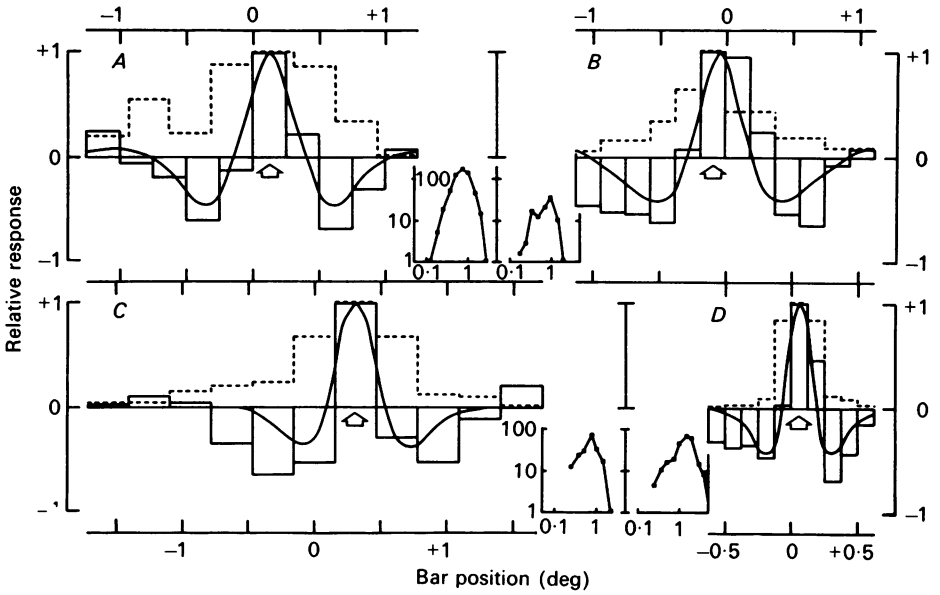

Fig. 9. A comparison among the observed line-weighting functions, the observed two-line interaction profiles and the predicted line-weighting functions of four complex cells. The conventions used in this figure are similar to those used in Fig. 6, except that the histograms drawn with continuous lines here represent normalized two-line interaction profiles, determined in each case with bar pairs of the same contrast polarity, while the histograms drawn with dashed lines represent the same neurones' line-weighting functions as determined with bars of the same polarity as those used in the two-line interaction experiments. The position of the conditioning bar for each two-line experiment is indicated by an arrow.

Comparison of two-line interaction profiles with grating responses

The two-line interaction profiles for complex cells seemed to deviate from the neurones' line-weighting functions in precisely the same way as did the line-weighting functions predicted from the neurones' responses to sinusoidal gratings. It was natural, then, to compare these two-line interaction profiles with the predicted line-weighting functions, and the results are illustrated in Fig. 9.

This Figure shows, for four complex cells, comparisons between two-line interaction profiles and line-weighting functions predicted from these neurones' spatial

frequency tuning curves. Both the predicted line-weighting functions and the two-line interaction functions have been normalized: for the two-line interaction functions, the maximum response obtained was assigned a value of 1·0, the response elicited by the conditioning bar alone was assigned a value of 0, and the other response magnitudes scaled accordingly. The inset graphs plot each neurone's spatial frequency

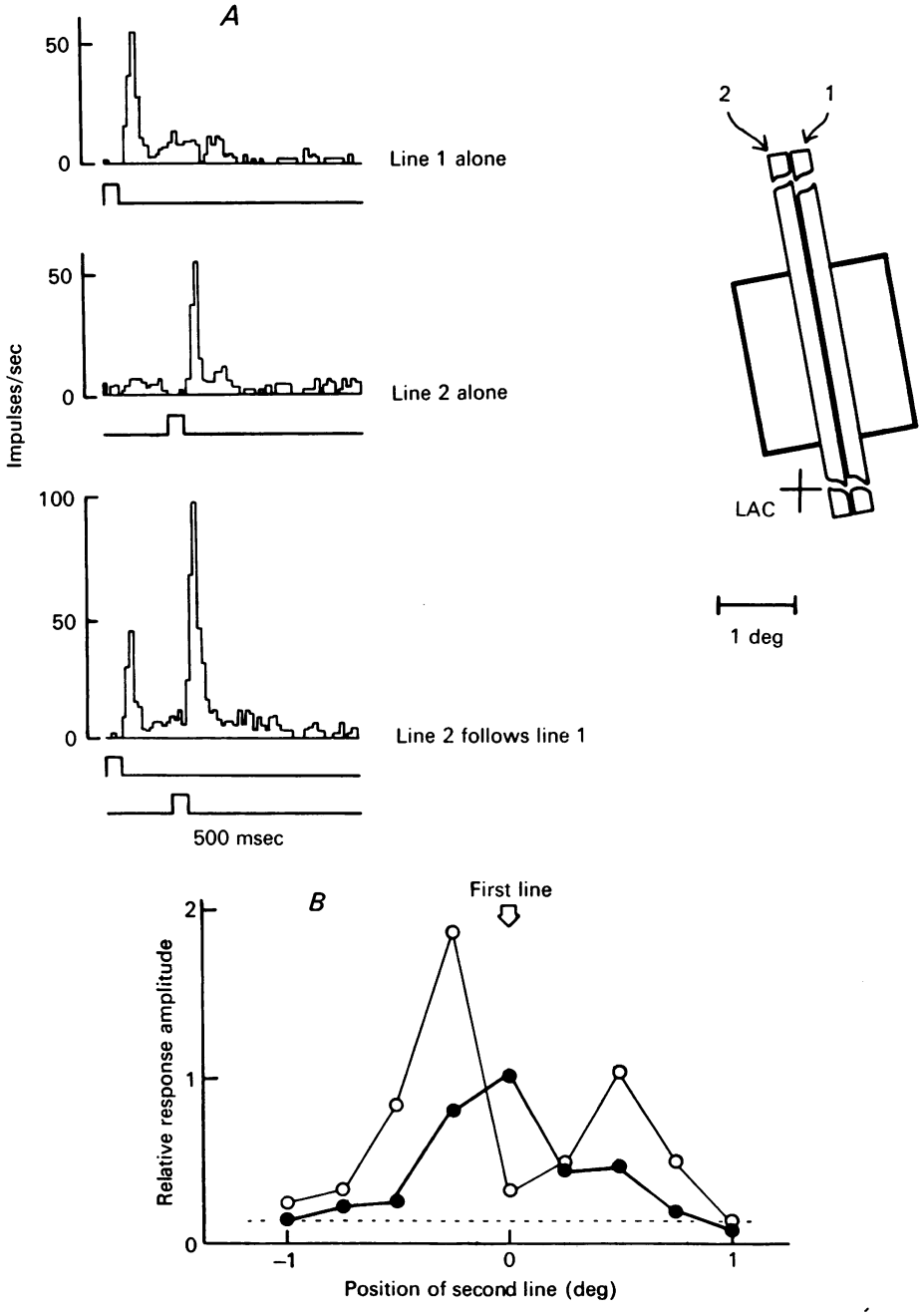

Fig. 10*A* and *B*. For legend see facing page.

tuning curve, and the dashed histograms show these same neurones' line-weighting functions for single lines of the same polarity used in the two-line interaction experiment. It is clear that these functions approach the prediction no more closely than they did for the complex cells shown in Fig. 6; the two-line interaction functions, however, provide a good fit to the predicted line-weighting functions. Note also that the two-line interaction profiles may exhibit subsidiary 'ripples' similar to those seen in the line-weighting functions of simple cells having relatively narrow spatial frequency tuning curves (Movshon *et al.* 1978*a*).

These two-line interaction profiles, then, represent in some way an accurate measure of the weighting function with which complex cells convolve a visual

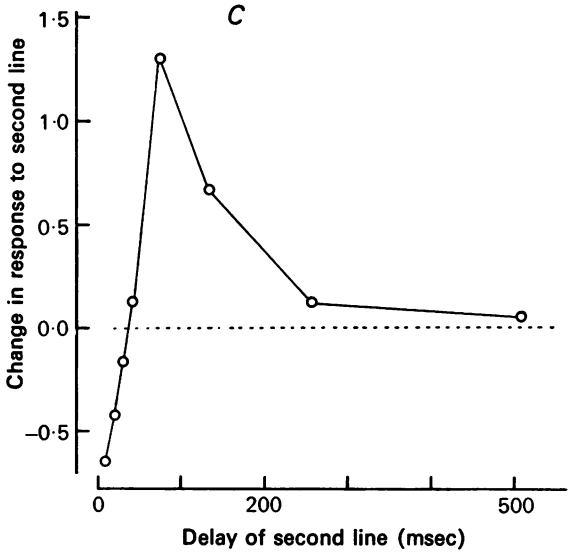

Fig. 10*C*.

Fig. 10. An experiment to determine the interaction between lines flashed in different positions at different times in the receptive field of a complex cell. *A*, on the right, the minimum response field and its position with respect to the left *area centralis* (LAC) are illustrated. Two lines of the width used in the experiment (0·25°) are drawn to scale; they were 10° long. On the left, the upper two histograms show the responses to these two lines presented separately for 32 msec once every second. The lowest histogram shows the response when line 2 was presented 125 msec after line 1. *B*, the filled symbols show the amplitude of the response to single lines (0·25° wide) presented separately at a variety of positions in the receptive field (0° on the abscissa is the centre of the field). The response amplitudes have been normalized to that of the central line, and the dashed line shows the spontaneous firing level. The open symbols show the response to lines presented in different positions when preceded by a conditioning line at position 0, indicated by the arrow. The delay between the two lines was 125 msec, and each line was presented for 32 msec. *C*, the change in response to a line caused by the previous presentation of a conditioning line 0·25° away in the receptive field as a function of the delay between the two lines. The dashed line indicates no change in response. The ordinate has been normalized to the response to the test line presented alone, so that 1·0 indicates a doubling of response amplitude. For delays greater than 64 msec, the responses to the two lines were distinguishable and the response to the second line is plotted. At shorter delays, the two responses merged; the value plotted is the response to the composite stimulus minus the sum of the responses to the conditioning and testing lines presented separately.

image. The fundamental constituents of complex cells may thus act in a manner similar to simple cells or more peripheral visual neurones. What gives a complex cell its special characteristics is not the manner of its visual filtering, but the way in which it combines many filtered samples over a substantial area of the visual field. These experiments indicate that each sample is made by a *subunit* of the complex cell receptive field. We will turn in the Discussion to the question of the origin of these subunits, and in the final part of this section we report some preliminary experiments designed to reveal the manner in which the subunits interact to generate the overall responses of complex cells.

Interactions between subunits

The existence of a number of discrete subunits within the receptive field of a complex cell invites comparison with the model proposed by Barlow & Levick (1965) to account for the directional movement selectivity of retinal ganglion cells in the rabbit. In this model, the ganglion cell's receptive field was held to contain multiple subunits, which moreover interact with one another over space and time in order to mould the cell's response as a function of direction of movement. Not only is the structure of this model similar to our own, but there is also a degree of similarity in receptive field structure between cortical complex cells and rabbit ganglion cells (see Wyatt & Daw, 1975; Daw & Wyatt, 1976).

Since one of the most obvious properties of cortical complex cells is commonly direction selectivity, and since the general subunit model seemed clearly capable of providing a mechanism to generate direction selectivity, we performed experiments on five complex cells that were modelled on those of Barlow & Levick; we examined the interactions between two-line stimuli presented asynchronously to different locations in the receptive field. The experimental paradigm is illustrated in Fig. 10*A*. A bright line, 10° long and 0·25° wide, was flashed on to the neurone's receptive field for 32 msec at the optimal orientation. The responses to two such lines, identical except for their position in the receptive field, are illustrated in the upper two histograms. The third histogram shows the cell's response to a combination of these two lines: line 2 was presented 125 msec after line 1. At this temporal delay, the neurone's responses to the two flashes can be discriminated as two distinct peaks in the histogram. The initial response (to line 1) was little different from that shown in the uppermost histogram. The later response (to line 2), however, was very much greater than the response to line 2 presented alone. The occurrence of a stimulus 125 msec earlier in a neighbouring part of the receptive field greatly increased the neurone's responsiveness to the second line.

The open circles in Fig. 10*B* show how the neurone's response to the second line varied with the spatial separation between the first (conditioning) line and the second (test) line. The conditioning line appeared throughout for 32 msec in the centre of the neurone's receptive field (0°); the abscissa shows the position of the test line, also presented for 32 msec but 125 msec later. For comparison, the filled symbols show the response to the test lines presented *without* a preceding conditioning stimulus. The response to the test line was greatly increased when it fell 0·25–0·75° from the conditioning line. The facilitation of response was greater when the test line fell to the left of the conditioning line; the neurone preferred stimuli moving to the left.

Fig. 10*C* examines the effect of the interval between flashes on the degree of facilitation. The spatial separation between the conditioning and test lines was 0·25°. The response to the test line was increased by the occurrence of the conditioning

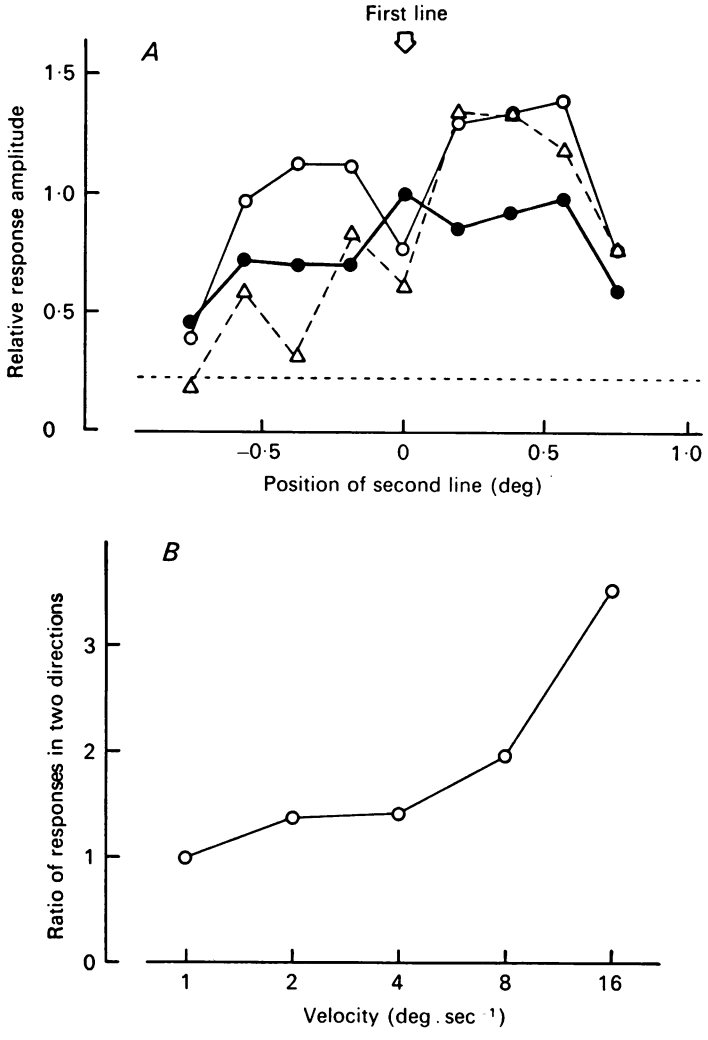

Fig. 11. *A*, as for Fig. 10*B* but for a second cell. The filled symbols show the response to single lines in a variety of positions. The open symbols show the response to a second line after a preceding conditioning line at position 0 (arrow). The delay between conditioning and testing lines was 125 msec (△) or 250 msec (○). Each line was presented for 32 msec and was 0·18° wide. *B*, the ratio of the amplitudes of the responses to lines moving through the receptive field in opposite directions is plotted against the speed of movement. The direction of movement was orthogonal to the preferred stimulus orientation for the neurone. The lines were again 0·18° wide.

line for inter-flash intervals between 50 and 200 msec. The reduced response at short delays is presumably due to the spatial weighting function of the individual subunits rather than to any interaction between subunits.

If the delayed facilitation of the response to stimuli in other parts of the receptive

field is related to the neurone's responses to moving stimuli, then we have sufficient data to estimate the neurone's optimal velocity of movement. The facilitation was greatest for spatial separations of about 0·25° and temporal delays of about 60 msec. The optimal moving stimulus should cover this distance in this time; i.e. at about 4°/sec. In fact, the optimal velocity of movement of a 0·25° wide bright line across the neurone's receptive field was about 3°/sec.

A further justification for supposing that this kind of facilitation is at least related to a neurone's preferences for speed and direction is given by the data in Fig. 11, obtained from a second complex cell. The upper graph shows how the response to the test line depended on its distance from the central conditioning line. The filled symbols again show the response to the test lines in the absence of a conditioning line. The open triangles show that, for a temporal delay between conditioning and test lines of 125 msec, facilitation was found only when the test line fell to the right of the conditioning line. But, at a longer delay (250 msec), faciliatation was almost as strong in the opposite direction (open circles). These results might suggest that at low velocities (equivalent to the long delay), the neurone should respond almost equally well to movement in the two directions. But at higher velocities, a marked preference for motion to the right should be evident.

The lower part of Fig. 11 reveals this prediction was at least qualitatively validated. The ratio of response in the two directions is plotted against the speed of movement of a bright line 0·18° wide. At velocities up to about 4°/sec, only a slight preference for rightward motion was evident; at higher velocities, the neurone showed a more marked preference for rightward motion.

These observations, which are typical of those we have made, show that there are delayed facilitatory interactions between the spatial subunits within the receptive fields of complex cells. We have no compelling evidence of delayed inhibition of the kind found in rabbit retina (Barlow & Levick, 1965; Wyatt & Daw, 1975), although our data are based on a limited sample of neurones.

DISCUSSION

Subunit organization in complex cell receptive fields

Our experiments on the responses of complex cells to pairs of lines revealed that these neurones appear to have a receptive field constructed from a number of subunits that *individually* seem to act in a more-or-less linear way. However, when tested conventionally, they behaved in a manner suggesting gross non-linearities of operation. If we are observing the properties of subunits during two-line interaction experiments, we may generate several hypotheses about the nature of these subunits, and the manner in which they combine to determine the complex cell's response.

The nature of subunits. Each subunit is organized into spatially separate antagonistic regions. This follows from the spatially antagonistic interaction profiles observed (Fig. 8), and from the fact that subunits appear to preserve information about the sign of the stimulus, since the profiles invert when stimulus polarity inverts.

The output of a subunit must be, to a first approximation, a linearly coded representation of the visual image. This follows from the correspondence between subunit profiles and line-weighting functions predicted from grating sensitivity (Fig. 9).

If subunits may be identified with the neurones that provide the afferent inputs to the complex cell, they may then be either lateral geniculate neurones or simple cortical neurones. It is possible that for different classes of complex cell the origin of the subunits may differ, with the properties of the subunit determining the behaviour of the complex cell.

For example the complex cells described by Palmer & Rosenquist (1974) which fail to show length summation within the receptive field and which have a much broader orientation tuning for a short bar than for a long bar might have geniculate afferents as their subunits as simple cells do not behave in this manner (Henry, Bishop & Dreher, 1974; Gilbert, 1977; Rose, 1977). A two-dimensional version of the two-line interaction experiment (a two-spot interaction experiment) should reveal radially symmetric subunits in this class of complex cell.

Differences in the nature of subunit input could also explain why complex cells behave in two distinct fashions when tested with binocularly disparate stimuli. Some cells behave as though they roughly add the response components produced by either eye alone (Pettigrew, Nikara & Bishop, 1968) whereas others show a tuning for binocular disparity much finer than suggested by their receptive field profiles (Pettigrew *et al.* 1968; Joshua & Bishop, 1970). It may be that the former possess monocular subunits whereas the latter possess binocular subunits, possibly derived from simple cells. If this is the case and our conjecture about the identity of subunits in Palmer & Rosenquist complex cells is correct then that type of complex cell should possess broad disparity tuning.

Interactions between subunits. If the complex cell's receptive field is composed of a number of discrete but spatially overlapping subunits whose properties are revealed by our two-line interaction experiments, how is the information from the different elements combined to produce the neurone's response? The simplest hypothesis is that the outputs of all subunits are rectified and added to provide the neurone's response (cf. Hochstein & Shapley, 1976*b*).

However, the spatially distributed nature of the subunit pool could provide a mechanism to generate the direction and movement selectivities of complex cells, if the subunits were connected in such a way that adjacent subunits could modulate each other's sensitivity. Our experiments with line pairs appearing asynchronously do, indeed, demonstrate appropriate interactions between complex cell subunits. In contrast to previous observation that the interactions involved in direction selectivity are inhibitory in nature (Barlow & Levick, 1965; Wyatt & Daw, 1975; Goodwin, Henry & Bishop, 1975; Goodwin & Henry, 1975; Sillito, 1975; Emerson & Gerstein, 1977), our evidence suggests that there are strong facilitatory interactions across the complex cell's receptive field (cf. Emerson & Gerstein, 1977). It is of course possible to generate directional selectivity using either scheme (see Barlow & Levick, 1965), and it is interesting that Sillito (1975) found that complex cells' direction selectivity sometimes survived ionophoretic application of bicuculline. It may be that complex cell directional selectivity is due to a combination of excitatory *and* inhibitory mechanisms, or is perhaps due only to facilitatory interactions of the kind we have observed.

We were surprised to observe facilitatory interactions in both directions away from our conditioning stimulus (e.g. Fig. 11), even though the effect was often greater in

one direction than the other. The possibility thus exists that the facilitatory mechanisms we have measured are not so much related to producing direction selectivity as they are to producing selectivity for *any* moving stimulus. Complex cells respond relatively poorly to stationary flashing stimuli, and it could be that it is the facilitatory interactions we have measured that give them their generally brisk responses to moving stimuli.

The precise form of the facilitation remains to be determined, but one attractive possibility is that it is multiplicative in nature (as if, for example, the activity of one subunit enhanced with some delay the effectiveness with which its neighbours influenced the neurone's discharge). The complex cell would then act as a spatial autocorrelator, a device well suited to movement detection (Poggio & Reichardt, 1976; Reichardt & Poggio, 1976; Foster, 1971).

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REFERENCES

BARLOW, H. B., BLAKEMORE, C. & PETTIGREW, J. D. (1967). The neural mechanism of binocular depth discrimination. *J. Physiol.* **193**, 327–342.

BARLOW, H. B. & LEVICK, W. R. (1965). The mechanism of directionally selective units in the rabbit retina. *J. Physiol.* **178**, 477–504.

CYNADER, M. S., BERMAN, N. & HEIN, A. H. (1976). Recovery of function in cat visual cortex following prolonged deprivation. *Expl Brain Res.* **25**, 139–156.

DAW, N. W. & WYATT, H. J. (1976). Kittens reared in a unidirectional environment: evidence for a critical period. *J. Physiol.* **257**, 155–170.

EMERSON, R. C. & GERSTEIN, G. L. (1977). Simple striate neurons in the cat. II. Mechanisms underlying directional asymmetry and direction selectivity. *J. Neurophysiol.* **40**, 156–173.

ENROTH-CUGELL, C. & ROBSON, J. G. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *J. Physiol.* **187**, 517–552.

FINLAY, B. L., SCHILLER, P. H. & VOLMAN, S. F. (1976). Quantitative studies of single cell properties in monkey striate cortex. IV. Corticotectal cells. *J. Neurophysiol.* **39**, 1352–1361.

FOSTER, D. H. (1971). A model of the human visual system in its response to certain classes of moving stimuli. *Kybernetik* **8**, 69-84.

GILBERT, C. D. (1977). Laminar differences in receptive field properties of cells in cat primary visual cortex. *J. Physiol.* **268**, 391–421.

GOODWIN, A. W. & HENRY, G. H. (1975). Direction selectivity of complex cells in a comparison with simple cells. *J. Neurophysiol.* **38**, 1524-1540.

GOODWIN, A. W., HENRY, G. H. & BISHOP, P. O. (1975). Direction selectivity of simple cells: properties and mechanism. *J. Neurophysiol.* **38**, 1500–1523.

HENRY, G. H., BISHOP, P. O. & DREHER, B. (1974). Orientation, axis and direction as stimulus parameters for striate cells. *Vision Res.* **14**, 767-777.

HOCHSTEIN, S. & SHAPLEY, R. M. (1976*a*). Quantitative analysis of retinal ganglion cell classifications. *J. Physiol.* **262**, 237–264.

HOCHSTEIN, S. & SHAPLEY, R. M. (1976*b*). Linear and nonlinear spatial subunits in Y cat retinal ganglion cells. *J. Physiol.* **262**, 265–284.

HUBEL, D. H. & WIESEL, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* **160**, 106–154.

JOSHUA, D. E. & BISHOP, P. O. (1970). Binocular single vision and depth discrimination. Receptive field disparities for central and peripheral vision and binocular interaction on single units in cat striate cortex. *Expl Brain Res.* **10**, 389–416.

MOVSHON, J. A., THOMPSON, I. D. & TOLHURST, D. J. (1978*a*). Spatial summation in the receptive fields of simple cells in the cat's striate cortex. *J. Physiol.* **283**, 53–77.

MOVSHON, J. A., THOMPSON, I. D. & TOLHURST, D. J. (1978*b*). Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. *J. Physiol.* **283**, 101–120.

PALMER, L. A. & ROSENQUIST, A. C. (1974). Visual receptive fields of single striate cortical units projecting to the superior colliculus in the cat. *Brain Res.* **67**, 27–42.

PETTIGREW, J. D., NIKARA, T. & BISHOP, P. O. (1968). Binocular interaction on single units in cat striate cortex: simultaneous stimulation by single moving slit with receptive fields in correspondence. *Expl Brain Res.* **6**, 391–416.

POGGIO, T. & REICHARDT, W. (1976). Visual control of orientation behaviour in the fly. Part I. Towards the underlying neural interactions. *Q. Rev. Biophys.* **9**, 311–375.

REICHARDT, W. & POGGIO, T. (1976). Visual control of orientation behaviour in the fly. Part II. A quantitative analysis. *Q. Rev. Biophys.* **9**, 377–438.

ROSE, D. (1977). Response of single units in cat visual cortex to moving bars of light as a function of bar length. *J. Physiol.* **271**, 1–23.

SHAPLEY, R. M. & HOCHSTEIN, S. (1975). Visual spatial summation in two classes of geniculate cells. *Nature, Lond.* **256**, 411–413.

SILLITO, A. M. (1975). The contribution of inhibitory mechanisms to the receptive field properties of neurones in the cat's striate cortex. *J. Physiol.* **250**, 304–330.

WYATT, H. J. & DAW, N. W. (1975). Directionally sensitive ganglion cells in the rabbit retina: specificity for stimulus direction, size and speed. *J. Neurophysiol.* **38**, 613–626.