J. Physiol. (1977), **271**, *pp.* 1–23
With 8 *text-figures*
Printed in Great Britain

RESPONSES OF SINGLE UNITS IN CAT VISUAL CORTEX TO MOVING BARS OF LIGHT AS A FUNCTION OF BAR LENGTH

By DAVID ROSE*

From the Physiological Laboratory, Downing Street, Cambridge CB2 3EG

(*Received 21st April 1976*)

SUMMARY

1. The responses of single units in the cat's primary visual cortex to moving bars have been examined quantitatively as a function of bar length.

2. For about half the cells studied, very long bars evoked weaker responses than short bars, implying that there were inhibitory regions flanking the receptive field centre. In another quarter of the cell sample, there was evidence of flanking regions which were facilitatory in effect.

3. The strength of the flanking regions was found to vary from cell to cell and there was no sudden transition between cells which were 'hypercomplex' and those which were not.

4. Within the central region of the receptive field, the responses of most (but not all) cells increased with bar length. About half the cells responded to very short bars or spots of light, but about one in six would not respond at all to short bars.

5. Correlations were sought between the properties of cells as simple or complex, their responsiveness to moving spots of light, the size of their receptive field centre and the polarity, strength and size of their receptive field flanks. Simple and complex cells with small receptive fields were more likely to respond well to spots, and to have strong inhibitory flanks.

6. Correlations were also sought between the above properties and several other parameters of cell behaviour. Cells with strong inhibitory flanks were found to be more broadly tuned for orientation. Individual cells were also more broadly tuned for the orientation of short bars than of long bars.

7. Evidence was obtained that spatial summation can be linear or non-linear for different cells.

* Present address: Department of Anatomy, The Medical School, University Walk, Bristol BS8 1TD

INTRODUCTION

In their classic studies of the activities of neurones in the visual cortex of the cat and monkey, Hubel & Wiesel (1962, 1965, 1968) classified cells on the basis of their responses to straight bars or edges of light flashing or moving in the visual field. Three types were distinguished: simple, complex, and hypercomplex, This final class was defined in terms of preference for bars or edges of a certain length, longer stimuli eliciting an attenuated response with respect to that elicited by an optimal length stimulus, such that most hypercomplex cells did not respond at all to very long bars. This suppression of the responses with increasing stimulus length was presumed by Hubel & Wiesel to be due to the activation of cortical inhibitory interneurones as the bar was extended to encroach upon regions flanking the receptive field.

More recent evidence, however, has indicated that the presence of such suppressive flanks is not an all-or-nothing phenomenon, but that their effect on cell firing is graded (Hubel, D. H., in discussion of paper by Bishop & Henry, 1972; Palmer, Rosenquist & Sprague, 1972; Rose, 1974; Bodis-Wollner, Pollen & Ronner, 1976; Wilson & Sherman, 1976). Also, those inhibitory processes which have been demonstrated physiologically in the visual cortex seem to function mainly to improve the selectivity of cells for the orientation and direction of movement of the stimulus (e.g. Creutzfeldt, Kuhnt & Benevento, 1974*a*; Rose & Blakemore, 1974*a*; Sillito, 1975) but may not greatly affect length specificity (Sillito & Versiani, 1976).

In this paper I report that the flanks of receptive fields in the visual cortex can, in some cases, even be facilitatory in effect. The functions of the flanks are further investigated by examining their effects on orientation specificity and other properties of receptive fields.

METHODS

General techniques

Adult cats (1·9–4·0 kg) initially prepared under sodium methohexitone (Brietal) anaesthesia were paralysed by continuous I.V. infusion of Flaxedil (10 mg/kg in 6 % (w/v) glucose solution, 4 ml./hr) and artificially ventilated with 80 % N_2O, 18 % O_2, 2 % CO_2 mixture (v/v). Body temperature was maintained at 37 °C, and EKG and EEG were monitored. Eye movements were suppressed both by the relaxant drug and by bilateral cervical sympathectomy. Eye rotation was assessed by photography of the slit pupils before and after surgery. Zero-power contact lenses prevented corneal drying and spectacle lenses focused the eyes on a tangent screen 57 cm away. Phenylephrine and homatropine were applied to retract the nictitating membranes and to dilate the pupils, and 3 mm diameter artificial pupils were substituted. The projections of the areae centrales were plotted on the screen daily using a reversible ophthalmoscope. A glass-insulated tungsten micro-electrode (as described by Levick,

1972, but with exposed tip length 14–20 μm) was introduced hydraulically through a small craniotomy to record extracellularly from units in the primary visual cortex, using conventional amplification and display techniques. Electrode positions were later verified histologically to be in area 17, often with the guide of up to four electrolytic lesions (5–10 μA for 5 sec) placed along each electrode tract.

Classification of receptive fields

Minimum response fields (Barlow, Blakemore & Pettigrew, 1967; Bishop & Henry, 1972) were plotted separately for each eye using back-projection on to the tangent screen. The dimension of the field perpendicular to the direction of movement of the optimal bar will be referred to here as the response field *length*, and the dimension of the field along the direction of movement will be termed the field *width*. The dimensions of the bar will be labelled similarly: *length* (perpendicular to direction of movement) and *width* (in direction of movement).

Cells were classified as simple, complex or hypercomplex according to criteria based on those of Hubel & Wiesel (1962, 1965). Receptive fields often contained one or more distinct areas, where a bright bar at the optimal orientation evoked a response when flashed either on or off; if there was spatial summation within a given 'on' or 'off' zone, then the cell was classified as simple. Complex cells gave no response to flashed stimuli or responded at 'on' and 'off' in all parts of the receptive field; as a class, these cells were more spontaneously active than simple cells, gave more spikes to a moving slit of light, often with a bursty response pattern, and responded well to higher velocities of movement. Hypercomplex cells responded weakly (or not at all) to long bars or edges, and the range of orientations to which the cell responded was often seen to be greater for short bars than for long. Ten of the sixteen hypercomplex fields which were plotted qualitatively contained areas responding well to short bars flashed on or off and filling one 'on' or 'off' zone, and like most simple cells these had very little spontaneous activity. As mentioned in the Introduction, a few cells responded strongly to long bars, but audibly even more strongly to short bars; a precise division between hypercomplex and non-hypercomplex could not be made, and the two of these cells which were studied quantitatively have been distinguished from other types in the Results. A fourth class of cell, termed 'pure direction-selective', was seen occasionally. These had some properties in common with the pure direction-selective cells of Blakemore & Van Sluyters (1974) and the corticotectal cells of Palmer, Rosenquist & Sprague (1972). They responded almost equally briskly to all stimuli moving in the preferred direction, even to spots or very short edges. Tested using long bars only, these cells would have been classified as complex on the basis of their high activity (spontaneous and evoked), large response field size, and on–off responses to flashed stimuli.

Quantitative methods

A bar of light was generated electronically on an oscilloscope (bar luminance was 30 cd/m^2, background 10 cd/m^2) and its orientation, width, direction and velocity of movement were adjusted to give as large and clear a response as possible, judged by ear. The bar was then moved across the receptive field of the cell in the dominant eye, and the number of action potentials was counted by gating a digital counter; the mean response to eight or more such presentations of the stimulus was then calculated. Spontaneous activity was assessed by counting spikes during the same gating period with the oscilloscope screen blanked. These data were then used to construct a length *tuning curve* for each cell.

Corrections for fluctuations in spontaneous activity and responsiveness

Fluctuations in spontaneous activity were controlled by measuring the maintained discharge several times throughout the period of data collection. The level of spontaneous firing was assumed to have been changing at a constant rate between one measurement and the next so that the number of spontaneous impulses which were counted during the intervening gating periods when the cell was being subjected to visual stimulation could be estimated by linear interpolation between the nearest immediately preceding and following measurements of spontaneous activity. The responses to visual stimuli could thus be expressed as *evoked* responses by subtraction of this estimated spontaneous discharge from the numbers of spikes counted during stimulation.

A standard length of the bar was chosen which would evoke a clear response: this was as long a bar as possible for most cells (15–17°), but only a few degrees or less for obviously hypercomplex cells. Fluctuations in responsiveness (Henry, Bishop, Tupper & Dreher, 1973; Rose & Blakemore, 1974*b*) were controlled by measuring the evoked response to this standard length of bar many times throughout the period of data collection. It was assumed that responsiveness had drifted linearly between the times of these measurements. Evoked responses to other lengths of bar (presented in pseudo-random order, and interspersed between the measurements of spontaneous activity and of responsiveness) were then expressed as a proportion of the magnitude of the evoked response to the standard bar, which was estimated in each case by linear interpolation between the nearest immediately preceding and following measurements of the standard evoked response.

Finally, the over-all level of spontaneous activity, and the over-all standard evoked response, were determined by averaging all their measurements taken throughout the whole period of data collection.

Fluctuations in spontaneous activity, and in responsiveness, were thus controlled independently, since in other experiments (unpublished) I have found that for different cells there may be negligible, mild or strong positive correlations between these two sources of response variability under similar experimental conditions. In most cells, about half the data collected were used to control these fluctuations. The use of linear interpolation is justified by the slowness of the fluctuations in comparison with the whole period of data collection.

The various properties of each cell estimated during the qualitative and quantitative analyses were later examined two by two for co-relationships using the χ^2, Student's t or product–moment correlation tests, as required by the parametric or non-parametric nature of the data.

RESULTS

The quantitative analysis was done on sixty-seven cortical cells and three identified LGN (lateral geniculate nucleus) fibres in seven cats, using stimuli of constant luminance. These cells all had response fields centred below the horizontal meridian and within 8° of the area centralis. They were stimulated with bars of light between $\frac{1}{8}$° and 17° in length.

Thirty-seven cells were classified on qualitative grounds as simple, sixteen as complex, and two as pure direction-selective. Ten cells were classed as hypercomplex, of which, by all criteria other than length selectivity, seven showed simple cell properties and three complex (Dreher, 1972). Two

cells were 'dubious hypercomplex', i.e. a confident decision could not be made as to whether these were hypercomplex or simple (one cell) or complex (one cell). These two dubious hypercomplex cells were indeed found, after quantitative analysis, to show a degree of length specificity which was near the borderline between cells which were classed as hypercomplex and those which were not (Figs. 2, 4), and for most of the subsequent analyses these two cells were classed with the simple and complex cells. In the searches for correlations between the different properties of cells to be described, the term *simple family of cells* will be used when simple cells are grouped with simple-type hypercomplex (forty-five cells) and the term *complex family* will refer to the combining of complex cells and complex-type hypercomplex (twenty cells); analyses including the two pure direction-selective cells will say so explicitly. This system of nomenclature is for convenience only and implies no special classification of pure direction-selective cells which may be considered a subclass of complex cells (see Methods).

The essential problem in testing the validity of the division of cortical cells into hypercomplex and non-hypercomplex types is that of determining what *is* the optimal length so that the response to this length can be compared with the response to a very long bar. Sampling errors, fluctuations in excitability which have not been fully compensated for, and the discreteness of sampling will all contribute to a discrepancy between the true optimal length and the optimal as determined empirically by presenting a series of bars of different lengths and simply defining the optimal as that length which evoked the largest response. In a preliminary report (Rose, 1974) the empirically determined best length was used in calculations of the relative responsiveness of cells to long and to optimal bars (the long/optimal response ratio). Smooth curves fitted by eye to each response *versus* length function (*length tuning curve*) are less affected by the sources of error just described and they will be employed in the present paper; some examples are shown in Fig. 2.

Classification of cells from their length tuning curves

The curves were classified primarily into three types, according to the effects on the cells' responses of extending the bar beyond the central region of the receptive field. In addition, the curves were classified again into three types depending on their responsiveness to very short bars crossing the receptive field centre. There were thus nine classifications: each class is illustrated in Fig. 1 and their frequencies of occurrence are presented in Table 1.

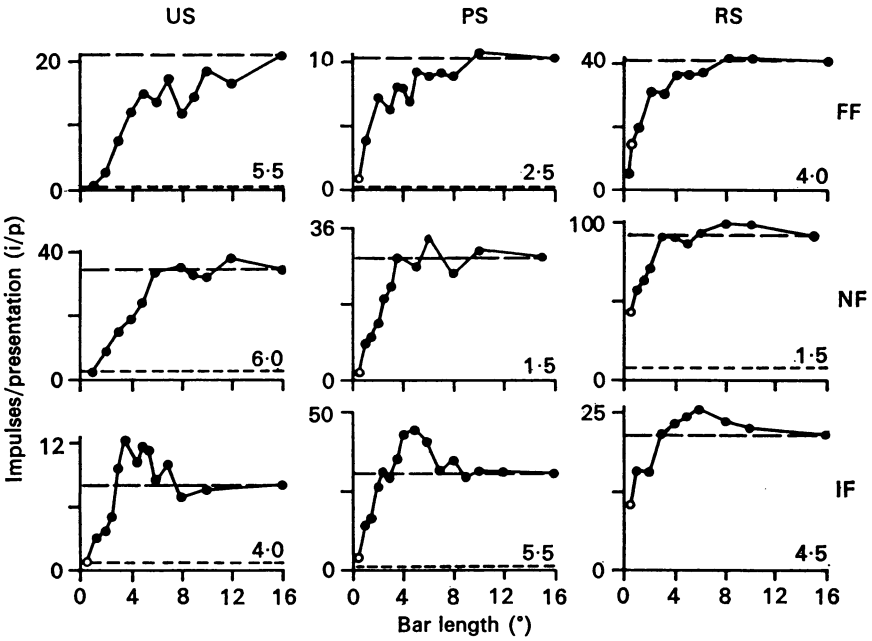

Fig. 1. Length tuning curves for cortical cells illustrating the two-way classification described in the text. Cells with facilitatory flanks (type FF) are shown in the top row, those with no flanks (type NF) in the middle row, and those with inhibitory flanks (type IF) in the bottom row. Cells which were unresponsive to small moving bars (type US) occupy the left-hand column, cells for which responses were directly proportional to bar length, up to a limit (type PS) are shown in the centre column, and cells responding well to very short moving bars (type RS) are presented in the right-hand column. All the cells illustrated were simple except for the middle and lower ones in the right-hand column (types NF–RS and IF–RS) which were complex. The frequencies of occurrence of each type of curve are shown in Table 1.

The response level to a long bar (long dashes) and the spontaneous firing level when greater than zero (short dashes) are shown to aid comparison of the other responses with them. Open symbols show responses to $\frac{1}{2}°$ long bars (when used) and the graphs have not been connected to zero length/spontaneous firing level, in order to facilitate comparisons of each cell's responsiveness to short bars. The distance of the response field centre from the projection of the area centralis is also shown in the lower right-hand corner of each graph, accurate to the nearest 0·5°.

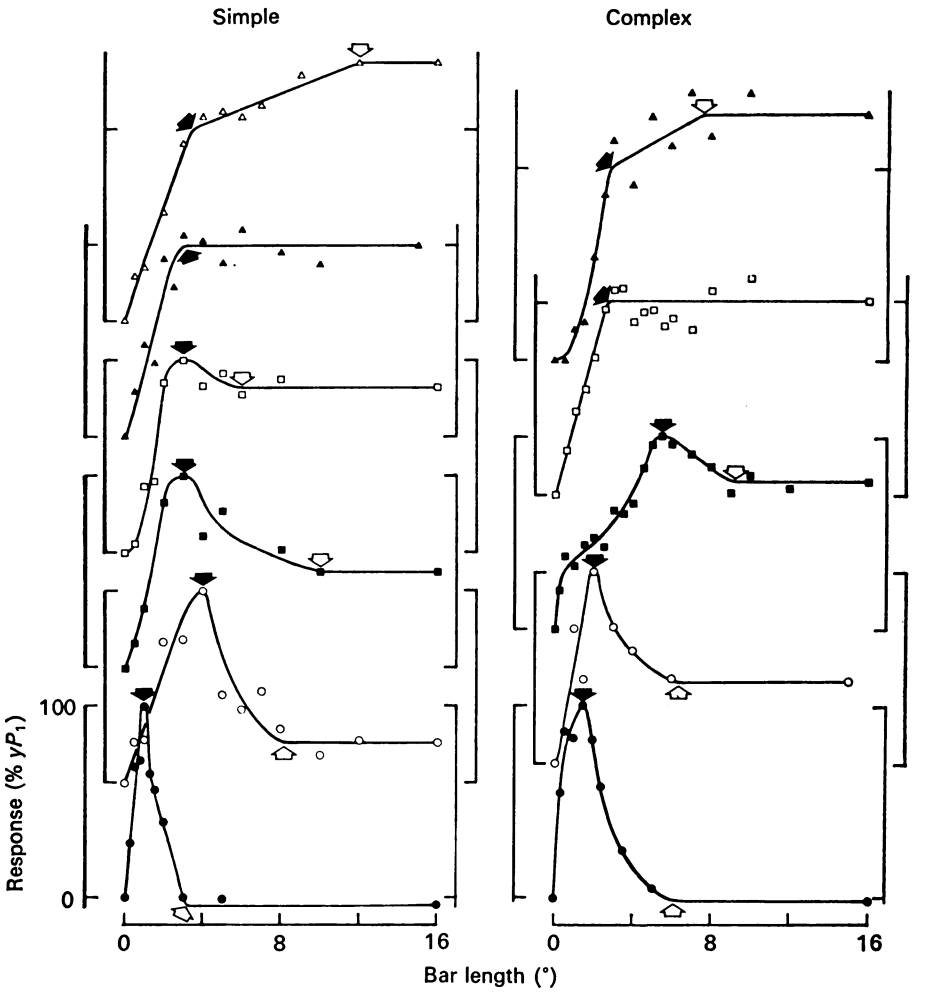

Fig. 2. Smooth length tuning curves fitted by eye. Responses shown are evoked spike counts (after subtraction of spontaneous firing) normalized to 100% at point P_1 (filled arrows; see text). Point P_2 is shown (where appropriate) by an open arrow. Simple-family cells are shown on the left, complex on the right. The bottom pair of curves (filled circles) are from cells classed qualitatively as hypercomplex; the pair above them (open circles) are from the two dubious hypercomplex cells which could not be classified by ear with certainty as hypercomplex; the remaining seven curves are from simple and complex cells. The top pair of curves are type FF, the next lowest type NF, and the rest type IF (*cf.* Fig. 1).

Classification by the nature of the flanks of the receptive field

Type NF: no flanks. The middle row of Fig. 1 shows the classical response pattern for simple and complex cells (e.g. Hubel & Wiesel, 1962). The response increased with bar length, often quite linearly, up to a point, P_1 (filled arrows in Fig. 2) beyond which the curve was flat. This pattern was seen in twenty cells (30%).

Type FF: facilitatory flanks. In the top row of Fig. 1 the pattern is similar up to point P_1, but beyond this there is a secondary, shallower *increase* in the response up to a point, P_2 (open arrows in Fig. 2). This totally unexpected pattern of responsiveness was seen in seventeen of the sixty-seven cells (25%).

TABLE 1. Classification of length tuning curves.

	Simple			Simple-type hyper-complex	Complex			Pure direction selective	Complex-type hyper-complex	LGN
	FF	NF	IF	IF	FF	NF	IF	IF	IF	IF
US	5	1	1	0	3	1	0	0	0	0
PS	4	7	6	1	0	2	1	0	0	0
RS	4	4	3	6	0	4	5	2	3	2
nc	0	1	2	0	1	0	0	0	0	1

The numbers of length tuning curves classified into each of the nine classes illustrated in Fig. 1 are shown according to cell type (simple, complex, etc.), identified as described in the Methods. Classifications according to the polarity of the receptive field flanks are : FF (facilitatory flanks), NF (no flanks) and IF (inhibitory flanks). Classifications according to the responsiveness to very small stimuli are: US (unresponsive to short bars), PS (responses directly proportional to length of short bar), RS (responsive to short bars) and nc (not classified owing to insufficient data about responses to very short bars).

Type IF: inhibitory flanks. The bottom row of Fig. 1 shows the pattern predicted in the Introduction, which was seen in thirty cells (45%). Over part of the curve, between points P_1 and P_2, there was a *decline* in response with increasing bar length. In some cells, the decline continued down to the zero response level.

The numbers of cells which were classified as types FF, NF or IF were not differently distributed between simple and complex cells ($\chi^2 = 0{\cdot}64$) nor between simple and complex families of cells (see preamble to Results; $\chi^2 = 0{\cdot}61$). Inclusion of pure direction-selective cells in the analysis makes little difference ($\chi^2 = 1{\cdot}16$ and $0{\cdot}91$ in the two cases, respectively). The occurrence of each type was not related to any artifactual cause, such as the stage of the experiment, nor to individual differences between cats.

Classification by responses to very short bars

A few cells in the cat's visual cortex respond well to moving spots of light and not just to long bars (Cynader, Berman & Hein, 1973; Henry, Bishop & Dreher, 1974*a*; Henry, Dreher & Bishop, 1974*b*; Olsen &

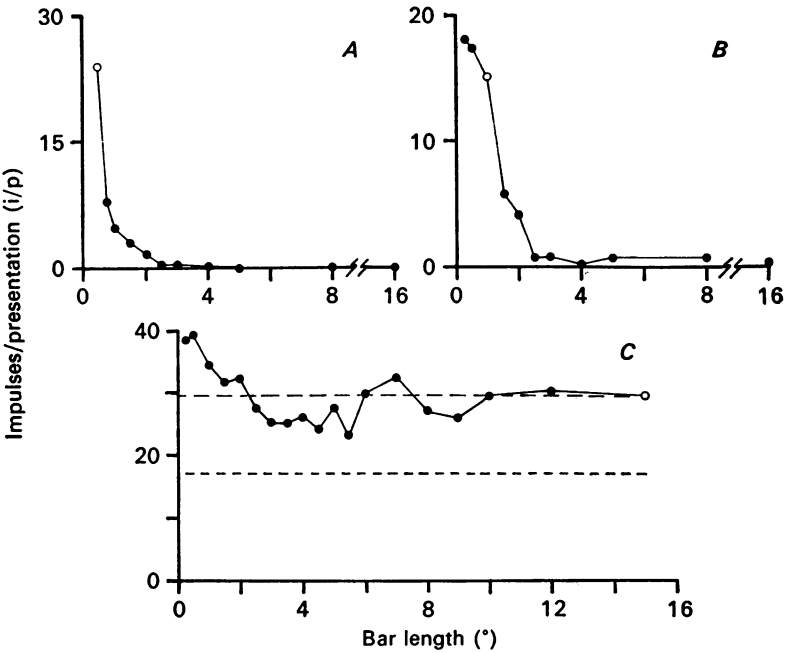

Fig. 3. *A*,*B*. Length tuning curves of two simple-type hypercomplex cells responding best to very small stimuli. Open symbols show bar length used to measure standard evoked response (see text). Qualitatively plotted response field lengths were 0·8 and 0·7° for *A* and *B*, respectively. *C*. Length tuning curve of an LGN afferent fibre. The cell was 'off'-centre, gave sustained responses to flashed stimuli, and had a high spontaneous activity (17 impulses/sec). It responded to stimuli presented to the ipsilateral eye. Its centre was found from qualitative plotting to be 2·8° in diameter, and was by far the largest of the fourteen LGN receptive field centres plotted during the present series. Spontaneous firing is shown by the lower (short) dashed line, and responses to long bars (the standard evoked response) by the open symbol and the upper (long) dashed line.

Pettigrew, 1974; Palmer & Rosenquist, 1974). Sixty-three of the cortical cells in my sample were stimulated with a range of very short bars, sufficient to enable the curves to be extrapolated back to zero length. The curves often passed above or below zero response, i.e. some cells responded briskly to very short edges, while other cells did not respond at all to such

stimuli. The cells were divided, therefore, for analysis into three types, each being illustrated in one column of Fig. 1.

Type PS: responses proportional to length of short bars (centre column of Fig. 1). For these cells the responses given were in direct proportion to the length of the bar (below point P_1).

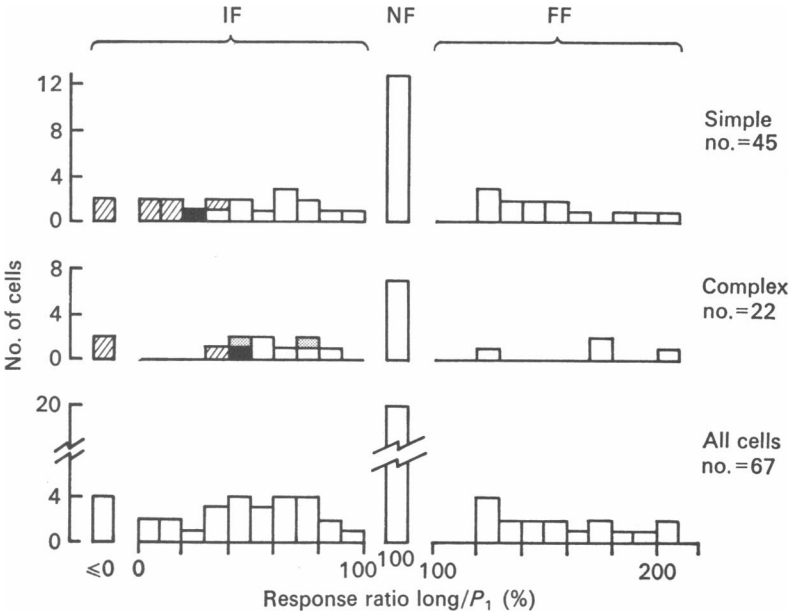

Fig. 4. Histograms showing the response to a bar (15–17°) as a percentage of the response to stimulation of the receptive field centre. The response from the centre has been taken from the y co-ordinate of point P_1 on the smoothed length tuning curve (see text and Fig. 2). Cells with facilitatory flanks (type FF) have long/centre response ratios of greater than 100%, those with no apparent flanks (type NF) have ratios of 100%, and for those cells with inhibitory flanks (type IF) the ratios are less than 100%; for three type IF cells, long bars suppressed spontaneous activity as well as the centre-evoked response (ratios $< 0\%$). Simple and complex families of cells are shown separately and combined. Hypercomplex cells are shown hatched and pure direction-selective cells stippled. The two dubious hypercomplex cells (classification uncertain from qualitative criteria alone, see text) are shown in black.

Type US: unresponsive to short bars or spots (left-hand column of Fig. 1). These cells did not respond to bars of $\frac{1}{2}°$ or less in length, and several required an even longer bar before a response could be elicited (up to 2°).

Type RS: responsive to spots (right-hand column of Fig. 1). The responses of these cells to bars $\frac{1}{2}°$ in length were greater than 25% of those to a bar

of optimal length. Several of them also responded very well to $\frac{1}{4} \times \frac{1}{4}$ degree square stimuli and even to $\frac{1}{8}°$ diameter spots, and for some the 'optimal' stimulus *was* a small spot, and not an extended edge at all (e.g. Figs. 3*A*, 3*B*, 8*B*)!

Of the sixty-three classifiable cortical cells, twenty-one were classed as type PS (33 %), eleven as type US (17 %) and thirty-one as type RS (49 %), see Table 1. The distribution between simple and complex cells does not differ significantly from chance ($\chi^2 = 4{\cdot}34$, d.f. = 2, $P < 0{\cdot}2$), even if hypercomplex cells or pure direction-selective cells or both are included ($P > 0{\cdot}05$).

Type US cells were commonly also type FF and vice versa, and types RS and IF were similarly associated (Table 1; the numbers are too low for χ^2 analysis, but if types NF and IF are combined, or types PS and RS, or both, then large values of χ^2 are obtained: $P < 0{\cdot}001$). Thus, on the whole, cells with inhibitory flanks respond well to spots and cells with facilitatory flanks require summation within the field centre before they will fire. These trends apply to simple as well as to complex cell families.

The hypercomplex cell classification

Hypercomplex cells have inhibitory flanks to one or both sides of the receptive field centre (Hubel & Wiesel, 1965, 1968). The data shown in Figs. 2 and 4 clearly indicate, however, that the presence of such flanks is not an all-or-nothing phenomenon. There is a continuous gradation of the effects of stimulating the regions beyond the receptive field centre, from profound inhibition (e.g. Fig. 8*B*), to no effect, and even to facilitation (type FF cells). All intermediate stages are represented. This applies both for the simple and for the complex cell groupings. Control experiments (see below) did not reveal any cells with an inhibitory flank on one side only.

In Fig. 4, there is no obvious level at which 'hypercomplex' cells end and the other cells (simple and complex) begin. A division could be made on the basis of either (*a*) whether the response to a long bar is not statistically above the spontaneous level of firing, in which case five cells of the present sample could be called hypercomplex, or (*b*) whether the response to a long bar is statistically below that to some shorter length, which is the case for thirty-three of the cells here. Clear divisions cannot, however, be made reliably by ear unless spontaneous activity is zero, for the judgement of thresholds depends on the signal-to-noise ratio at a time when the signal is very small. The noise may, in this instance, be equated with spontaneous firing, which varies both from cell to cell and from time to time (Pettigrew, Nikara & Bishop, 1968; Henry *et al.* 1973; Rose & Blakemore, 1974*b*).

The adjective 'hypercomplex' will be used throughout the rest of this

paper to refer to cells with extremely strong inhibitory flanks. The usage coincides to a certain extent with the traditional notion of hypercomplexity (Hubel & Wiesel, 1965; Dreher, 1972) but recognizes that the term refers to a quantitative extreme, and not to a qualitatively separate group of cells. For convenience, those cells which were classified by ear as hypercomplex will be separated off whenever the properties of cells with extremely strong inhibitory flanks are to be examined.

Quantitative measures from the length tuning curve

The x co-ordinate of point P_1 on the length tuning curve has been taken as an indication of the diameter (length) of the receptive field *centre*, while the x co-ordinate of point P_2 has been taken as a measure of the size of the *flanks* adjacent to the centre. The strength of the flanks has been assessed by comparing the values of the y co-ordinates of points P_1 and P_2, i.e. by calculating the ratio between the number of spikes evoked from the field centre and from the centre and flanks stimulated together using a long bar (the *long/P_1 response ratio*).

The stability of these parameters over time was established in a number of cells which were recorded for several hours.

The strength of the receptive field flanks. The distributions of this parameter for simple and complex cell families are shown in Fig. 4. There are no real differences in the shapes, means or extents of the distributions for simple or complex cells, nor for the cell families.

The length of the receptive field centre. There were no differences in the lengths of the receptive field centres between simple, complex and pure direction-selective cells (means = 3·75, 3·76 and 3·50°, respectively) but for the simple- and complex-type 'hypercomplex' cells the centres were smaller (means = 1·27 and 1·20°). Fig. 5 shows the correlation that exists between the strength of the inhibitory flanks (when present) and the length of the receptive field centre: strong inhibitory flanks are clearly associated with short field centres ($r = 0{\cdot}71$, $P < 0{\cdot}001$) and this holds true even if simple or complex cells, or cell families, are taken alone. The more responsive the cell was to spots, the shorter its receptive field centre. Centre length increased with distance of the field from the area centralis.

The quantitatively determined length of the receptive field centre exceeded that of the minimum response field as plotted by hand in fifty out of sixty-five simple- and complex-family cells (77 %). In one case only, the field plot was so much larger than the optimal stimulus (Fig. 8) that the quantitative determination cannot be taken as a valid estimate of the size of the field 'centre'.

The length of the receptive field flanks. Type FF cells had longer flanks over-all than type IF (means 8·9° and 6·3°, respectively, $t = 3{\cdot}69$; $P <$

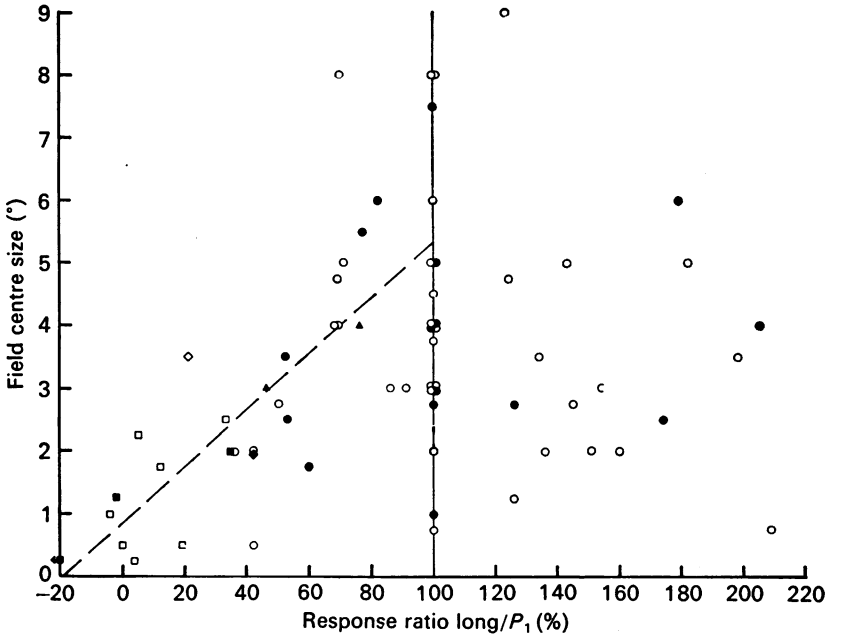

Fig. 5. Length of receptive field centre as a function of flank strength. The ordinate shows the x co-ordinate of point P_1 (Fig. 2) on the length tuning curve, while the ratio between the y co-ordinates of points P_1 and P_2 is plotted along the abscissa as a % of the value at point P_1 (P_2 is assumed level with P_1 for type NF cells). Type IF cells have ratios of less than 100 %, for type FF cells the ratios are greater than 100 %, and the type NF cells fall on the 100 % line. The extreme cell shown in Fig. 10, whose spontaneous activity was greatly inhibited by long bars, is represented here by a symbol with an arrow attached; this cell has been excluded from the correlations reported in this paper between flank strength and the other cell parameters. The regression line for centre size on flank strength for type IF cells is dashed in ($r = 0{\cdot}71$; $n = 29$; $P < 0{\cdot}001$); the corresponding correlation for type FF cells is not significant.

Simple-family cells are shown by open symbols, complex-family by filled symbols. Cells classified qualitatively as hypercomplex are represented by squares, the two dubious hypercomplex cells (see text) by diamonds, pure direction-selective cells by triangles, and the remaining simple and complex cells by circles.

0·001); this was true also for simple or complex cells separately. The stronger the flanks of type IF cells, the shorter they were, and cells responsive to spots also had short flanks. Flank size was positively correlated with field centre size, both for type FF and IF cells.

Correlations with other properties of cortical cells. There were no significant correlations of the above parameters of length tuning curves with

spontaneous activity, evoked activity (y co-ordinate at point P_1), velocity preference or direction preference, although these other properties did differ between simple and complex cells in accordance with previous reports (Pettigrew *et al.* 1968; Rose & Blakemore, 1974*b*; Ikeda & Wright, 1975; Movshon, 1975; Singer, Tretter & Cynader, 1975). Correlations were present, however, with ocular dominance (type FF cells were usually monocularly dominated, as were types US and PS cells) and with orientation specificity. The *range* of orientations of the bar to which the cell would respond was measured routinely during the initial qualitative plotting. This qualitative measure correlates well with the breadth of orientation tuning as estimated quantitatively ($r = +0{\cdot}62$; $P < 0{\cdot}001$; data from sixty-eight orientation tuning curves taken from these and other experiments using similar methods). Cells with strong facilitatory flanks tended to be narrowly tuned for orientation (trend not significant among type FF cells), while cells with strong inhibitory flanks responded over a wide range of orientations (among type IF, $r = 0{\cdot}49$; d.f. $= 28$; $P < 0{\cdot}01$) even if 'hypercomplex' and pure direction-selective cells were excluded (r then $= 0{\cdot}47$; $P < 0{\cdot}05$). Simple and complex cells were similar in this respect.

Experiments using non-optimal stimuli

For several cells, the effects of altering the contrast, velocity or direction of movement of the stimulus were investigated. The tuning curves were affected only in their response amplitude and not in their other quantitative characteristics, nor over-all shape. The curves obtained using a single edge stimulus were also similar in pattern for either polarity of edge.

Length tuning curves were similar in shape in each eye for three simple cells, but the non-dominant eye was relatively unresponsive to very short bars. For two pure direction-selective cells the long/P_1 response ratio was lower in the non-dominant eye, which had a smaller receptive field for one of the cells.

For six cells, orientation tuning curves (Rose & Blakemore, 1974*b*) were constructed using two or more different lengths of bar. In all cases, orientation tuning was found to be broader when short bars (less than the size of the field centre) were used. Fig. 6 shows the results from a simple cell. The response field plot in the dominant eye is shown in Fig. 6*A*, and the length tuning curve in Fig. 6*B*: the cell had facilitatory flanks. In Fig. 6*C*, the orientation tuning curves are presented for very long bars (open circles), bars the same size as the field centre (filled triangles) and bars even shorter than this (filled circles); this last curve is broader and flatter than the other two. One other simple cell was similar, but for three (complex family) type IF cells the orientation tuning curves were higher,

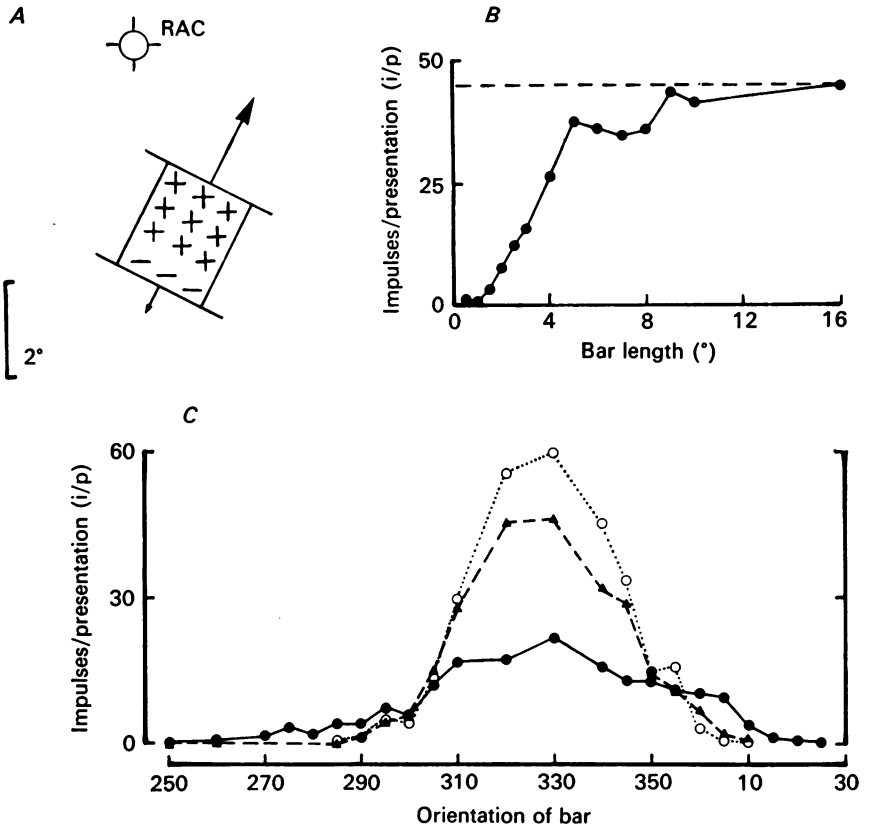

Fig. 6. *A*. Min. response field of a simple cell which responded only to stimuli presented to the right (contralateral) eye. The projection of the right area centralis (RAC) is shown as a circle with true horizontal and vertical, corrected for eye rotation. Plus signs show regions of the field from which transient responses were evoked when a bright bar was flashed on; minus signs show an area responding at bar off. The cell preferred upward movement to downward (note relative sizes of arrows). Spontaneous activity was zero throughout. *B*. Length tuning curve for bars at an orientation of 330°. (Orientation code for this Fig. and Fig. 7*C*: 0° = horizontal bar moving upward; 90° = vertical bar moving to the left; 180° = horizontal bar moving downward; 270° = vertical bar moving to the right.) The cell was unresponsive to short bars and had facilitatory flanks. *C*. Orientation tuning curves for bars 2½° long (filled circles and continuous lines), 5° (filled triangles and dashed lines) and 16° (open circles and dotted lines). The responses to the three lengths of bar were measured successively (in randomized order) at each orientation. The cell responded to very long bars and to bars of 5° length (the same size as the field centre as estimated from the length tuning curve) over the same range of orientations, but it was tuned more broadly for the orientation of shorter bars.

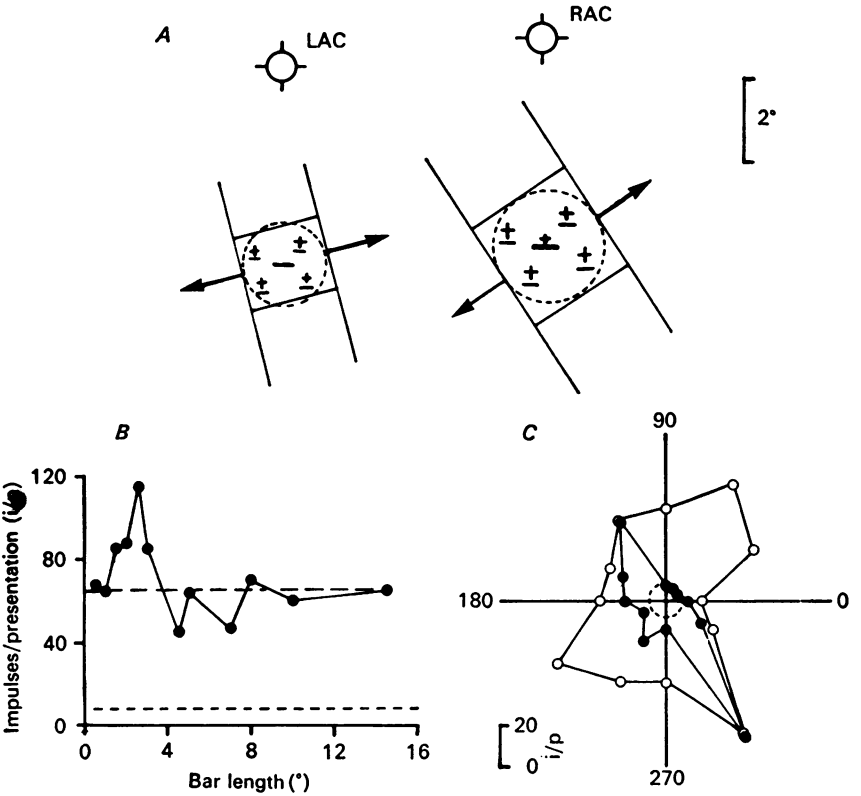

Fig. 7. *A*. Receptive field plots for an unusual, probably complex, cell. The rectangular areas are the minimum response fields plotted using long moving bars. The cell responded best to bars tilted anticlockwise from vertical and moving in either direction (arrows). The right (ipsilateral) eye was more effective than the left. Within the dashed circular areas the cell would also respond to small spots. Flashing a stationary spot produced transient responses at both on and off in most parts of the receptive field, but the off responses were clearly predominant in the centre of the circular area. Small moving spots, brighter or darker than the background, would also evoke responses when moved *in any direction* within the circular areas. *B*. Length tuning curve for the right eye for bars tilted 30° anticlockwise from vertical and moving to the right (orientation 300°, see legend to Fig. 6*B*). Short dashes show the spontaneous firing level (2·1 impulses/sec), long dashes, the standard evoked response (see text). The cell responded just as well to bars ½° long as to 14½°. However, the best responses of all were to bars 2½° long, about the same size as the plotted receptive field; there was summation within the field and an inhibitory surround. *C*. Orientation tuning curves plotted on polar co-ordinates for the right eye using bars 17° long (filled symbols) and ½° long (open symbols). Spontaneous firing (dashed) was 2·0 impulses/sec for both curves. See legend to Fig. 6*B* for orientation code. i/p = impulses per stimulus presentation (radial axis).

as well as broader, for short bars. One further complex cell was studied, the results being presented in Fig. 7 in a similar manner to those in Fig. 6. This cell was an extreme example of the principle, in that it was almost completely non-orientational for very short bars (open symbols in the polar plot of Fig. 7*C*), yet narrowly tuned for the orientation of long bars (filled symbols in Fig. 7*C*). Some similar results have been reported by Henry *et al.* (1974*a*,*b*).

For four simple cells and one complex cell, the length tuning curves were re-assessed with the bar at up to eight non-optimal orientations. There were no changes in the properties of the curve (apart from response amplitude) except that away from the optimal orientation the long/P_1 response ratio fell, as follows from the broader orientation tuning of cells to short bars (Fig. 6*C*, and Henry *et al.* 1974*a*, Fig. 5, and 1974*b*, Fig. 6).

Component parts of the receptive field and their interactions

Three further quantitative methods were used for plotting the receptive fields of twelve cells (though not all of these cells were analysed using all three methods).

1. A very short bar was moved through the receptive field but its line of movement was displaced laterally after 8–10 presentations to stimulate different parallel strips of the receptive field.
2. A very short bar with one end always moving along the line bisecting the minimum response field was, after every 8–10 presentations, extended by a small amount at its peripheral end only. Thus, one half of the receptive field was not stimulated at all and the other half was stimulated more and more from the centre outwards.
3. An initially short bar, passing well to one side of the field centre, was extended gradually to form a very long bar crossing the whole receptive field (see insets to Fig. 8). This is similar to the method used to plot the lateral borders of the minimum response field qualitatively (Barlow *et al.* 1967; Bishop & Henry, 1972).

For all three paradigms, the bar was presented at the optimal orientation, the total number of spikes fired as the bar traversed the field was counted, and the stimuli were actually presented in pseudo-random order, i.e. the bar's extent or position was not changed gradually across the field. Paradigms 2 and 3 were repeated for each side of the receptive field, making five sets of data in all.

The estimate of the length of the centre of the receptive field from the length tuning curve was verified using these procedures (except for the cell shown in Fig. 8).

There were no obvious asymmetries in the strengths, nor the sizes, of the flanks on each side of the field centre.

Although the initial segment of the length tuning curve often rose linearly up to point P_1 (Figs. 1, 2), summation was strictly only linear if the cell was of type PS. Only then was the response to stimulation of the

whole central region with a single bar the same size as the centre found to equal the sum of the responses to stimulating separate areas with shorter bars, so as to cover exactly the same central region. For type RS cells, the former response was less, and for type US cells greater, than the sum of the responses to the shorter bars.

Summation of the centre and flank components must also be non-linear, because facilitatory flanks do not (by definition) fire the cell when stimu-

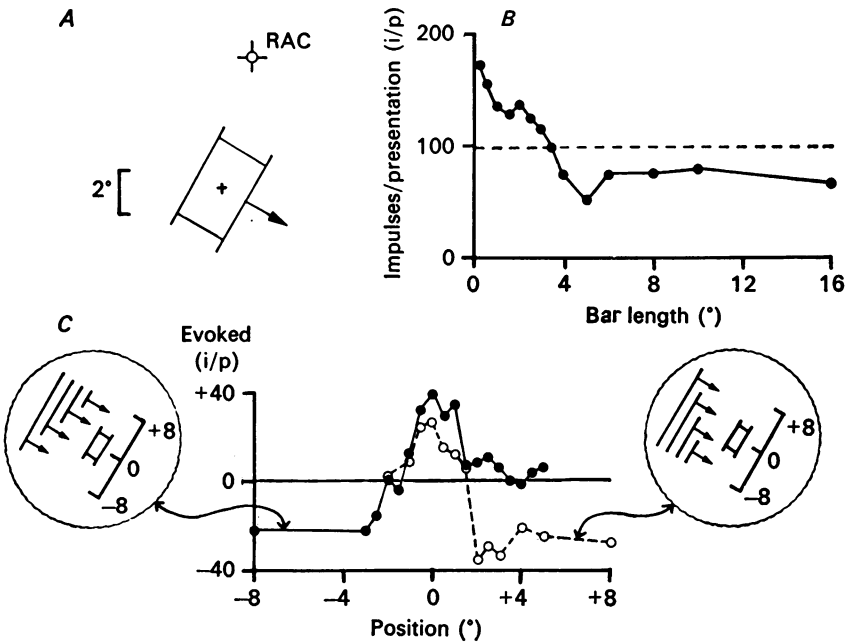

Fig. 8. *A*. The min. response field of a complex-type hypercomplex cell studied in the right (ipsilateral) eye (the left eye gave a very similar response field plot). The cell had a very high and irregular spontaneous discharge but prolonged 'on' responses to flashed stimuli were still audible in the centre of the response field. *B*. Length tuning curve for bars centred on the response field in the right eye. *The dashed line shows the spontaneous firing level*. Bars of 4° or longer inhibited the spontaneous discharge (which was 33 impulses/sec). *C*. A quantitative receptive field plot using paradigm 3 as explained in the text. Bars were extended across the receptive field, first from one side and then from the other, as shown diagrammatically in the insets. The abscissa shows the position of the extended end of the bar. The responses shown are the evoked spike counts relative to the spontaneous firing as zero (i/p = impulses per presentation). Differences in the absolute values of comparable evoked responses between the length tuning curve shown in *B* and the two receptive field curves shown here are due mainly to drifts in responsiveness between the times at which the data for these three curves were collected.

lated alone, and nor do inhibitory flanks suppress spontaneous firing when they are stimulated in isolation (results from three cells).

In Fig. 8 are shown the results from a complex-type hypercomplex cell with very high spontaneous discharge which was inhibited by long bars (the dashed line in the length tuning curve, Fig. 8*B*, shows the spontaneous firing level). The receptive field plotting procedures presented in Fig. 8*C* show that stimulation of either flank alone did not affect cell firing, that stimulation of one flank and part of the centre evoked an excitatory response, but that stimulation of all components of the field simultaneously with a long bar inhibited the cell. The inhibitory 'flanks' of this cell seemed, therefore, to be co-extensive with and about the same size as the excitatory 'centre'; the centre was more responsive to small stimuli but the inhibitory mechanisms summated with increasing bar length at a faster rate, or saturated less quickly.

Lateral geniculate neurones

The afferent axons of three lateral geniculate neurones were recorded just below the cortex, and length tuning curves were constructed just as for the cortical cells, but with the stimulus bar horizontal. All three cells were 'off' centre, two of them giving sustained responses to flashing stimuli and one transient. The length tuning curves were all type IF, and the two cells studied with a range of short bars responded very well indeed to spots (type RS). The fibre studied in most detail is illustrated in Fig. 3*C*. A similar pattern for LGN cells has been reported by Dreher & Sanderson (1973).

DISCUSSION

The receptive field flanks

An unexpected component in the structure of cortical receptive fields has been demonstrated by the present experiments: that of facilitatory flanks. The possible artifactual origin of these in the increasing amount of light scattered by longer bars can be refuted by their obvious presence in some cells in a control sample, which were stimulated using bars of constant total light flux. It is also highly unlikely that scattered light would facilitate the responses, since for most cortical cells the optimal stimulus is a narrow bar with clear, sharp edges, and broad or blurred stimuli are not as effective.

Facilitation can also be seen in some cortical cells when an optimal moving grating stimulus is extended along its axis of movement into those areas of the visual field which are traversed by an optimally orientated short bar just before it enters, and just after it leaves, the excitatory receptive field (Maffei & Fiorentini, 1976). These results and my own, taken together, suggest that facilitation is not limited to the end-zones, but

might be derived from anywhere within the region surrounding the receptive field centre.

Figs. 2 and 4 support the idea that the effects of the flanking areas of receptive fields may be graded along a continuum from profound inhibition to marked facilitation, passing through a null-point where no flanks are apparent. It is, however, difficult to imagine how one single neural mechanism could underlie such a phenomenon. The obvious modification to the hypothesis, then, is to suggest that the receptive fields have both inhibitory and facilitatory components in their flanks, and that the strength of each component can vary independently from nought upwards, and the over-all effect of stimulating the flanks depends on the *balance* between the two factors. Thus cells with no apparent flanks might, in fact, have strong inhibitory and facilitatory inputs of approximately equal potency.

The surround regions of cortical cells were stimulated by Blakemore & Tobin (1972) and Fries & Albus (1973), who found that this either inhibited or did not affect cell firing; neither group reported facilitation. The total amount of inhibition evoked by the complete surround grating that these workers used may have been greater than the total amount of facilitation; the latter might only be revealed under conditions of partial stimulation of the surround regions such as occurs with a single bar stimulus.

Inhibitory regions in simple cell receptive fields have been described by Bishop, Coombs & Henry (1973), and it has been proposed (Henry *et al.* 1974*b*) that these regions sharpen the orientation tuning for long bars relative to that for short bars (Figs. 6, 7). However, the receptive field plan of Bishop *et al.* (1973) applies only for moving stimuli, and does not explain the orientation selectivity of simple cells for stationary flashing bars (Henry *et al.* 1974*a*; own unpublished results). The inhibitory side bands of Bishop *et al.* (1973) are, therefore, probably part of the receptive field 'centre' as distinct from the 'flanks', and the side bands may function more to improve spatial frequency specificity or stimulus localization, rather than orientation tuning. (I will discuss this point more fully in a subsequent paper, in preparation.)

Spatial summation in the visual cortex

Spatial summation in the LGN may or may not be linear for different cells (Ikeda & Wright, 1976; Shapley & Hochstein, 1975), but in the cortex such investigations have only been applied to the effects of extending the *width* of a flashing stimulus, i.e. increasing its size along the preferred axis of movement. Thus, simple cells show linearly increasing responses within one 'on' or 'off' area, and decreasing responses if both areas are stimulated, while complex cells respond only to very narrow flashing bars and not to broader ones (Hubel & Wiesel, 1962; Toyama, Maekawa &

Takeda, 1973; Movshon & Tolhurst, 1975). If summation is symmetrical in all directions across the receptive field, then simple cells should show summation along the bar's length (the initial section of the length tuning curve should have a positive slope) and complex cells should respond to spots or very short bars only. This is clearly not the case; both simple and complex cells may show summation or they may respond well to spots, and both simple- and complex-family cells have been found which respond best of all to spots (Figs. 3, 8). There is thus some anisotropy of summation across the receptive fields of many cortical cells.

Cell families in the visual cortex

Both anatomical and physiological evidence (e.g. Szentagothai, 1973; Toyama, Matsunami, Ohno & Tokashiki, 1974; Singer *et al.* 1975) shows that many neurones in the cat's visual cortex must receive their main excitatory drive from within the cortex itself and not from the LGN afferents directly. Do these second-order neurones have more elaborate receptive fields which differ sharply from those of their inputs, possessing (for instance) complex or hypercomplex properties, as suggested by the hierarchical model of Hubel & Wiesel (1965, 1968)? Complex and hypercomplex properties are certainly not restricted to these second-order neurones (Hoffman & Stone, 1971; Movshon, 1975; Singer *et al.* 1975) and the data presented in this paper show that hypercomplex cell properties do not appear suddenly, but may be present to varying extents in different cells; hypercomplex cells are just extreme examples of simple or complex cells.

The neurones in area 17 thus fall broadly into two groups or 'families', simple and complex, which may derive some of their basic properties from their subcortical inputs (Movshon, 1975; cf. Singer *et al.* 1975) and which pass on these properties to other cells in the same family. Within each family we may look for gradual changes in properties between cells driven mainly by LGN inputs at one extreme, and at the other, those dominated by other cortical cells (Singer *et al.* 1975). Cells with mixed simple–complex properties do occur (e.g. Hubel & Wiesel, 1962; Kelly & Van Essen, 1974) but, on the whole, the interactions between these families are either weak (from simple to complex: Blakemore & Van Sluyters, 1975; Movshon, 1975) or inhibitory (from complex to simple: Creutzfeldt *et al.* 1974*a*; Creutzfeldt, Innocenti & Brooks, 1974*b*; Innocenti & Fiore, 1974; Movshon, 1975; Singer *et al.* 1975).

I am greatly indebted to Dr Colin Blakemore for his valuable help and advice throughout this work. I am also very grateful to Drs J. A. Movshon and R. Williams for their comments on the manuscript, and to R. D. Loewenbein, J. S. Dormer, A. Featherstone, C. A. Wood, D. Ellis and M. Appleby for their assistance. The

author was supported by a scholarship from the M.R.C., and the equipment was provided by the H. E. Durham Fund and M.R.C. grant No. G972/463/B to C. Blakemore.

REFERENCES

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

BISHOP, P. O., COOMBS, J. S. & HENRY, G. H. (1973). Receptive fields of simple cells in the cat striate cortex. *J. Physiol.* **231**, 31–60.

BISHOP, P. O. & HENRY, G. H. (1972). Striate neurons: receptive field concepts. *Investve Ophth.* **11**, 346–354.

BLAKEMORE, C. & TOBIN, E. A. (1972). Lateral inhibition between orientation detectors in the cat's visual cortex. *Expl. Brain Res.* **15**, 439–440.

BLAKEMORE, C. & VAN SLUYTERS, R. C. (1974). Reversal of the physiological effects of monocular deprivation in kittens: further evidence for a sensitive period. *J. Physiol.* **237**, 195–216.

BLAKEMORE, C. & VAN SLUYTERS, R. C. (1975). Innate and environmental factors in the development of the kitten's visual cortex. *J. Physiol.* **248**, 663–716.

BODIS-WOLLNER, I. G., POLLEN, D. A. & RONNER, S. F. (1976). Responses of complex cells in the visual cortex of the cat as a function of the length of moving slits. *Brain Res.* **116**, 205–216.

CREUTZFELDT, O., INNOCENTI, G. M. & BROOKS, D. (1974*b*). Vertical organization in the visual cortex (area 17) in the cat. *Expl. Brain Res.* **21**, 315–336.

CREUTZFELDT, O. D., KUHNT, U. & BENEVENTO, L. A. (1974*a*). An intracellular analysis of visual cortex neurones to moving stimuli: responses in a co-operative neuronal network. *Expl. Brain Res.* **21**, 251–274.

CYNADER, M., BERMAN, N. & HEIN, A. (1973). Cats reared in stroboscopic illumination: effects on receptive fields in visual cortex. *Proc. natn. Acad. Sci. U.S.A.* **70**, 1353–1354.

DREHER, B. (1972). Hypercomplex cells in the cat's striate cortex. *Investve Ophth.* **11**, 355–356.

DREHER, B. & SANDERSON, K. J. (1973). Receptive field analysis: responses to moving visual contours by single lateral geniculate neurones in the cat. *J. Physiol.* **234**, 95–118.

FRIES, W. & ALBUS, K. (1973). Centre-surround in receptive fields of neurones in the cat's striate cortex. *Pflügers Arch. ges. Physiol.* **339**, *R*93.

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

HENRY, G. H., BISHOP, P. O., TUPPER, R. M. & DREHER, B. (1973). Orientation specificity and response variability of cells in the striate cortex. *Vision Res.* **13**, 1771–1779.

HENRY, G. H., DREHER, B. & BISHOP, P. O. (1974*b*). Orientation specificity of cells in cat striate cortex. *J. Neurophysiol.* **37**, 1394–1409.

HOFFMANN, K-P. & STONE, J. (1971). Conduction velocity of afferents to cat visual cortex: a correlation with cortical receptive field properties. *Brain Res.* **32**, 460–466.

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.

HUBEL, D. H. & WIESEL, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *J. Neurophysiol.* **28**, 229–289.

HUBEL, D. H. & WIESEL, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *J. Physiol.* **195**, 215–243.

IKEDA, H. & WRIGHT, M. J. (1975). Retinotopic distribution, visual latency and orientation tuning of 'sustained' and 'transient' cortical neurones in area 17 of the cat. *Expl Brain Res.* **22**, 385–398.

IKEDA, H. & WRIGHT, M. J. (1976). Properties of sustained-X, transient-Y and transient-X cells in the cat's lateral geniculate nucleus (LGN). *J. Physiol.* **254**, 65–66*P*.

INNOCENTI, G. M. & FIORE, L. (1974). Post-synaptic inhibitory components of the responses to moving stimuli in area 17. *Brain Res.* **80**, 122–126.

KELLY, J. P. & VAN ESSEN, D. C. (1974). Cell structure and function in the visual cortex of the cat. *J. Physiol.* **238**, 515–547.

LEVICK, W. R. (1972). Another tungsten microelectrode. *Med. & biol. Engng*, **10**, 510–515.

MAFFEI, L. & FIORENTINI, A. (1976). The unresponsive regions of visual cortical receptive fields. *Vision Res.* **16**, 1131–1139.

MOVSHON, J. A. (1975). The velocity tuning of single units in cat striate cortex. *J. Physiol.* **249**, 445–468.

MOVSHON, J. A. & TOLHURST, D. J. (1975). Linear and nonlinear behaviour in cat striate cortical neurones. *Expl Brian Res.* Suppl. **23**, 146.

OLSEN, C. R. & PETTIGREW, J. D. (1974). Single units in visual cortex of kittens reared in stroboscopic illumination. *Brain Res.* **70**, 189–204.

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.

PALMER, L. A., ROSENQUIST, A. C. & SPRAGUE, J. M. (1972). Corticotectal systems in the cat: their structure and function. *Corticothalamic Projections and Sensorimotor Activities*, ed. FRIGYESI, T. L., RINVIK, E. & YAHR, M. D., pp. 491–523. New York: Raven.

PETTIGREW, J. D., NIKARA, T. & BISHOP, P. O. (1968). Responses to moving slits by single units in cat striate cortex. *Expl Brain Res.* **6**, 373–390.

ROSE, D. (1974). The hypercomplex cell classification in the cat's striate cortex. *J. Physiol.* **242**, 123–125*P*.

ROSE, D. & BLAKEMORE, C. (1974*a*). Effects of bicuculline on functions of inhibition in visual cortex. *Nature, Lond.* **249**, 375–377, 869.

ROSE, D. & BLAKEMORE, C. (1974*b*). An analysis of orientation selectivity in the cat's visual cortex. *Expl Brain Res.* **20**, 1–17.

SHAPLEY, R. & 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 striate cortex of the cat. *J. Physiol.* **250**, 305–329.

SILLITO, A. M. & VERSIANI, V. (1976). Synaptic mechanisms contributing to the length preference of hypercomplex cells. *J. Physiol.* **263**, 171–172*P*.

SINGER, W., TRETTER, F. & CYNADER, M. (1975). Organization of cat striate cortex: a correlation of receptive-field properties with afferent and efferent connections. *J. Neurophysiol.* **38**, 1080–1098.

SZENTAGOTHAI, J. (1973). Synaptology of the visual cortex. *Handbook of Sensory Physiology*, vol. VII/3, part B, ed. JUNG, R., pp. 269–324. Berlin: Springer-Verlag.

TOYAMA, K., MAEKAWA, K. & TAKEDA, T. (1973). An analysis of neuronal circuitry for two types of visual cortical neurones classified on the basis of their responses to photic stimuli. *Brain Res.* **61**, 395–399.

TOYAMA, K., MATSUNAMI, K., OHNO, T. & TOKASHIKI, S. (1974). An intracellular study of neuronal organization in the visual cortex. *Expl Brain Res.* **21**, 45–66.

WILSON, J. R. & SHERMAN, S. M. (1976). Receptive field characteristics of neurones in cat striate cortex: changes with visual field eccentricity. *J. Neurophysiol.* **39**, 512–533.