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RECEPTIVE FIELDS OF SIMPLE CELLS IN THE CAT STRIATE CORTEX

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SUMMARY

1. The excitatory and inhibitory components in the receptive fields of unimodal simple cells in the striate cortex of the cat anaesthetized with nitrous oxide have been described using slits of light and single light-dark edges as stimuli.

2. There is a small excitatory region (excitatory complex) centrally located in the receptive field that is made up of various combinations and spatial arrangements of subliminal excitatory and discharge subregions or centres.

3. The subliminal excitatory centres were revealed by a binocular facilitation technique. The excitability of the cell was raised by repeated stimulation via one eye while the neurone was tested with single edges via the other eye.

4. The subliminal excitatory and discharge centres are each specifically activated by only one type of edge, light-dark or dark-light, and then only in one direction of motion. All the subregions in the excitatory complex have the same optimal stimulus orientation.

5. Inhibitory components in the receptive field were identified by stimulating the cell with bars of light and single edges against an artificial background discharge produced by repeated stimulation separately applied either to the same eye (monocular conditioning) or to the other eye (binocular conditioning). There are powerful inhibitory sidebands to either side of the excitatory complex and these inhibitory regions merge to include the excitatory complex when stimulus orientation is angled away from the optimal.

6. Excitation is highly stimulus specific whereas inhibition is non-specific.

7. The organization of the two receptive fields of a binocularly discharged cell can be closely similar.

8. The attempt is made to translate the concept of subliminal excitatory and discharge centres into specific neural mechanisms involving both the geniculo-cortical input and various intracortical circuits.

9. These new developments call for only minor modifications to the model we have proposed for the organization of the receptive field.

INTRODUCTION

The basic stimulus for a simple cell in the striate cortex of the cat is an optimally oriented single light–dark border or edge moving in the preferred direction, the region or regions in the receptive field from which firing can be obtained being referred to as *discharge centres* (Bishop, Coombs & Henry, 1971*a*). In the same publication we also described the spatial organization of these discharge centres. Simple cells are classified as unimodal, bimodal or multimodal according to the number of spatially discrete discharge centres within their receptive fields. Even for a unimodal simple cell, the discharge centre is, in fact, a complex of centres since each type of edge, light and dark, may have its own separate subcentre (i.e. light edge discharge centre or dark edge discharge centre) in one or both directions of stimulus movement. For this reason we now propose to call the main excitatory region the *excitatory complex* of the receptive field.

By appropriate facilitatory stimuli applied to the excitatory complex, it is possible to reveal further subregions or centres which are ordinarily only subliminally excited by the basic stimulus. We shall refer to such regions as *subliminal excitatory centres*. In addition to describing subliminal excitatory centres as additional components in the excitatory complex, the present paper will also describe the inhibitory components in the receptive field. Our earlier observations on binocular interaction on single striate cells of the unimodal type (Henry, Bishop & Coombs, 1969; Bishop, Henry & Smith, 1971*c*) enabled us to predict that either to one or both sides of the excitatory complex there are powerful *inhibitory sidebands* averaging about 2° across. Using quite different methods we are now able to confirm these predictions. Simple cells show little or no spontaneous activity so that we have made extensive use of an artificial background discharge to disclose both the subliminal excitatory centres and the inhibitory regions (cf. Henry *et al.* 1969; Bishop, Coombs & Henry, 1971*b*; Henry & Bishop, 1972).

While the receptive field organization is described in terms of subliminal excitatory and discharge centres and inhibitory regions, in Discussion the attempt will be made to translate these concepts into specific neural mechanisms involving both the geniculo-cortical input and various intra-

cortical circuits. These new developments call for only minor modifications to the model we have proposed for the organization of the receptive field (Bishop *et al.* 1971*b*).

METHODS

Our general experimental methods have been described in detail elsewhere (cf. Bishop *et al.* 1971*a*; Bishop & Henry, 1972). Cats were anaesthetized with ether for the initial surgical procedures and subsequently with N_2O/O_2 (70%/30%). Eye movements were reduced to a very low level by complete paralysis of the animal, combined with bilateral cervical sympathectomy (Rodieck, Pettigrew, Bishop & Nikara, 1967; Kinston, Vadas & Bishop, 1969). The Horsley–Clarke horizontal of our stereotaxic apparatus is tilted forward by 12·5° so as to bring the visual axis parallel to the floor and perpendicular to the tangent screen. Single units in the striate cortex were recorded with glass insulated tungsten micro-electrodes (Levick, 1972) centred on the cortical projection of the visual axis (Horsley–Clarke co-ordinates posterior 3·0 mm, lateral 2·0 mm – Joshua & Bishop, 1970). Careful placement of the micro-electrode is important because, in this way, the area of search on the plotting table can be limited to within 3° (5·3 cm at 1 m) of the visual axis. The properties of each receptive field were explored by hand at the plotting table so as to determine as far as possible the optimal stimulus parameters to be used in the subsequent quantitative studies. These preliminary studies usually required about half an hour for each cell.

Quantitative study of the properties of the receptive fields was carried out by moving bars of light ('slits') over a rear projection screen placed usually at 2 m, and occasionally 4 m, in front of the nodal points of the cat's eyes. Records of the single unit responses were obtained in the form of average response histograms (e.g. Fig. 6) generated by a specially modified RIDL Multichannel Analyser. Driven at a constant, but optimal, velocity by the triangular waveform from a function generator, the testing slit was moved forwards and backwards right across the whole of the receptive field of the unit under examination. In each histogram the stimulus turn-round point is indicated by a vertical arrow. A pulse synchronous with the start of the wave form triggered the multichannel scaler at the onset of each sweep. A second pulse, synchronous with the end of the rising phase of the triangular waveform, was stored in the analyser to mark the bin corresponding to the end of the forward sweep. Usually 20 stimulus sweeps were enough to produce a satisfactory average response histogram when only the testing stimulus was used.

Because simple cells have little or no spontaneous activity we made use of an artificial background discharge to reveal the subliminal excitatory and inhibitory regions in the receptive field (Henry *et al.* 1969; Henry & Bishop, 1971, 1972). This background discharge was produced by the movement of a narrow ($< 0{\cdot}3°$) conditioning slit whose velocity was again optimal, or nearly so, but whose sweep was of small amplitude and confined to the immediate vicinity of the discharge centre. Each time the conditioning stimulus moved in the preferred direction it produced a burst of spikes which, after sufficient repetition and in the absence of the testing stimulus, ultimately filled the bins in the scaler fairly uniformly (Fig. 3*A*). The filling was uniform because the spike discharge caused by the conditioning stimulus was random with respect to the cycling of the multichannel scaler. As we have already mentioned, the recycle pulse for the scaler always came from the function generator used to drive the testing stimulus, and the function generator for the conditioning stimulus operated asynchronously to it. Inhibitory regions in the receptive field are readily demonstrated against this artificially induced background discharge by having the two slits, conditioning and testing, operating at the same

time. The conditioning and testing stimuli can both be applied to the same eye (*monocular conditioning*) or separately to the two eyes (*binocular conditioning*). When binocular conditioning was used, the stimulus for each eye was strictly confined to that eye by placing a septum between the two eyes and by increasing, with prisms, the divergence due to paralysis of the extraocular muscles. While the results obtained by these two procedures are similar there are, however, important differences (see below). A satisfactory histogram obtained by either procedure requires a total of about 4000 spikes. Typically we use 100 testing stimulus cycles during which time there might be between 500 and 600 cycles of the conditioning stimulus.

For details regarding our stimulus conventions see Bishop *et al.* (1971*a*). The abscissae of the average response histograms are scaled in analyser bins (e.g. 0–199) or alternatively in either spatial units (e.g. cm on the tangent screen or degrees of visual angle) or temporal units (e.g. sec). The ordinates of the histograms are scaled in spikes/sec averaged over one analyser bin in each case. The term *mean response* is used of the firing frequency in spikes/sec averaged over the 5 analyser bins centred on the bin containing the maximum count. For a tangent screen at 2 m, 1° visual angle = 3·5 cm.

RESULTS

In order to gain a general understanding of the nature of the receptive field organization it has been necessary to piece together information obtained from many hundreds of cells. While the data available from any one cell was usually not sufficiently diverse to provide a reasonably complete picture of its specific organization, we do, nevertheless, have a number of cells where the very prolonged recording and the wide range of the data we obtained have enabled us to reconstruct the receptive field organization of the particular cell in some detail. We have chosen one of these cells (6–1–2) to form the main basis of our descriptions in this paper. The amount of data available from this cell also provides the opportunity for a quantitative examination of the relationship between the various features of the receptive field organization. Part 1 below will be concerned with cell 6–1–2 and Part 2 with unimodal simple cells in general.

PART 1

Cell 6–1–2

Spatial organization of excitatory complex

The recordings from cell 6–1–2 were made fairly continuously over a period of about 9 hr and yielded a total of forty-two histograms, a selection of which are used for Figs. 1–6 inclusive. When only the test stimulus was used, the usual histogram (20 sweeps) took about 5 mins to prepare for and record, but it took 10 min or more for a histogram like those in Fig. 3 (50 sweeps) when both conditioning and testing stimuli were in operation. As shown in Fig. 6*A*, cell 6–1–2 reacted to the movement of an optimally

oriented narrow (0·29°) slit with an approximately equal response from the two eyes. The responses in Fig. 6*A* are presented as continuous line histograms rather than the usual bar histograms. The cell was classified as a unimodal simple cell, and in this connexion at least, there is probably no significance in the slight double peak in each of the two responses. Although the length of the slit traverse was exactly the same for the two directions of stimulus movement (i.e. 7·1°), in this and all the other Figures illustrating cell 6–1–2, the forward and backward portions of the histograms are of slightly unequal length. This results from the fact that, in this particular experiment, the adjustment of the function generator driving the galvanometer mirrors was such that the time taken for the forward movement was very slightly less than for the reverse direction. The duration of each channel (bin) in the multichannel scaler was always the same (in this case 50 msec) but because of the inadvertent setting of the function generator the first 'half' of the histograms had 95 bins and the second 102 (Fig. 2*A*). This slight change in the velocity of the slit was without physiological significance but allowance had to be made for it in the interpretation of our results, particularly in relation to the spatial arrangement of the excitatory centres.

As we have already indicated, the term *excitatory complex* refers to the combination of centres, both discharge and subliminal excitatory, that are to be found within the one small region of the visual field. The excitatory complex for cell 6–1–2 was made up of four centres consisting of one discharge centre and three subliminal excitatory centres, the discharge centre being for the light (leading) edge on the forward sweep. The first step towards elucidating the nature and spatial arrangement of these excitatory centres was to record from the right eye a series of histograms in response to slits of different width, three histograms from the series being selected for Fig. 1. These records differ from those in Fig. 6*A* in that the testing stimuli (slits of different width) have been applied against a background discharge produced by monocular conditioning (see Methods and legend for details). The relatively low levels of the background discharge in Fig. 1 (compared with Fig. 3), though partly due to the inhibitory effect of the width of the slit in relation to the sweep amplitude, was mainly the result of the small number of testing sweeps (20 sweeps) that were used for these histograms. The background discharge is built up from brief randomly occurring bursts of impulses so that the time taken for 100 testing sweeps is usually necessary for the conditioning stimulus to accumulate an adequate background sample. Fifty testing sweeps were used for the histograms in Fig. 3.

In the series in Fig. 1 we always kept the starting position of the dark edge on the forward sweep constant. The discharge peaks on the forward

sweep can thus be ascribed to the light edge since they shifted their bin location in close agreement with the changing position of the light edge. There was therefore a light edge discharge centre for this direction of movement. With the reversal of the stimulus movement at the end of the forward sweep, the dark (trailing) edge of the slit for the forward direction became the light (leading) edge on the backsweep (cf. Bishop *et al.* 1971*a*). In every histogram except that for the 1·14° slit there was also a small 'peak' near the middle of the backsweep. Since this peak did not change its bin location with change in slit width, the conclusion is that it, too,

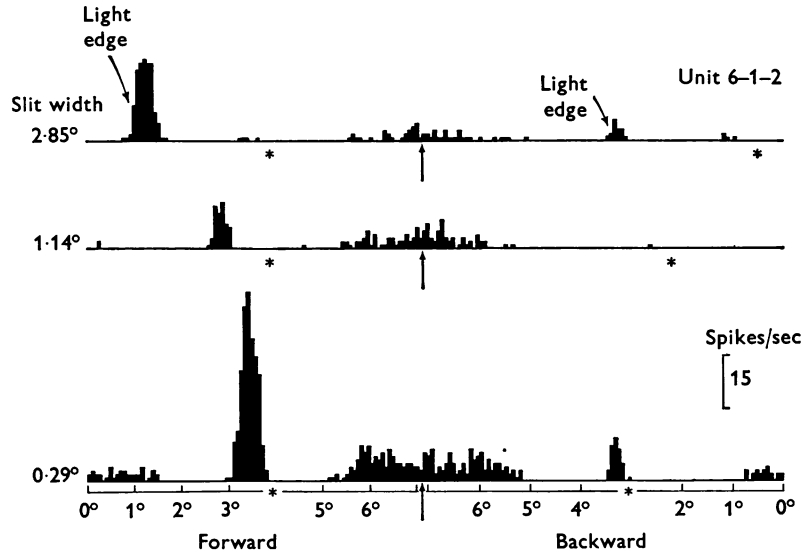

Fig. 1. Average response histograms from unit 6–1–2 selected from a series in response to optimally oriented slits of different width moved at 1·4°/sec forward and backward over the receptive field for the right eye, each histogram being recorded against a background discharge produced by monocular conditioning. Vertical arrows in this and subsequent figures indicate the stimulus turn-round point. Starting location of the dark edge on the forward sweep kept constant throughout. With monocular conditioning the cell responds only to the light edge and the expected location of a dark edge discharge is indicated by an asterisk in each case. Each histogram sums 20 testing sweeps using 200 channels at 50 msec/channel. Same cell as for Figs. 1–6 inclusive.

must have been produced by movement of the light edge. Although we have referred to this response on the backsweep as a 'peak' it actually rises little or not at all above the level of the background discharge. It appears as a small peak in these histograms simply because of the absence of any background discharge to either side of it. We have applied the term

inhibitory sidebands to these regions where the background discharge is absent (Bishop *et al.* 1971*c*). These sidebands, which are described in more detail below, are seen more clearly in Fig. 3*B* where the discharge peak on the backsweep barely reach (at orientation 160°) or rise above (at 152°)

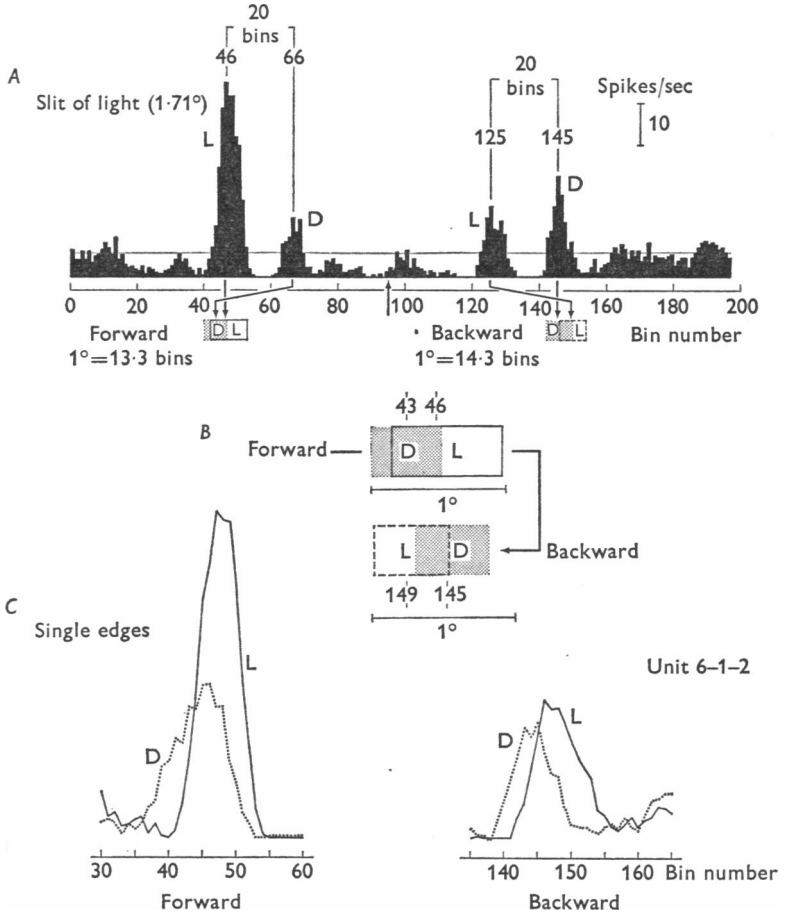

Fig. 2*A*. Average response histogram (right eye test) to a wide slit (1·71°) showing that, with binocular conditioning, cell 6–1–2 responded to both edges, light (L) and dark (D), in both directions of stimulus movement. Dotted line: mean level of background discharge.

B, relative locations of discharge centres for the dark edge (stippled rectangles, D) and the light edge (open retangles, L) for forward and backward movement of the edges. Numerals indicate analyser bins corresponding to the discharge peaks (as in Fig. 3*A*). Stippled and open dashed rectangles are centres normally subliminal to monocular stimulation.

C, portions of average response histograms to single light (L) and dark (D) edges shown in full in Fig. 6 showing that the dark edge discharge peak precedes the light edge discharge for both directions of stimulus movement.

the level of the background discharge. Reference to Fig. 6*A* shows that the test stimulus by itself caused occasional spikes near the middle of the backsweep and we can now say these almost certainly occurred in response to the light edge of the slit.

By contrast there is no evidence in the histograms in Fig. 1 of any discharge due to the action of the dark edge in either direction of movement. The asterisks indicate the expected locations of the dark edge discharges had they occurred. Nevertheless, the presence of subliminal excitatory centres for the dark edge are clearly demonstrated when they were facilitated by the technique of binocular conditioning. With this method the background discharge is produced by a conditioning stimulus applied to the eye opposite to the one used for the test stimulus. In Fig. 2*A* the test stimulus was applied to the right eye and the conditioning stimulus to the left. The test slit was wide enough (1·71°) so as to produce, for each direction of stimulus movement, two discharge peaks (L and D) that were clearly separated from each other. Since the first peak in each half of the histogram corresponds to the expected location of the light edge discharge (cf. Fig. 1), it is therefore likely that the second peak in each half is produced by the dark edge. Although, for both directions of stimulus movement, the discharge peaks were separated by 20 bins (Fig. 2*A*), the slit width was equivalent to 23 bins on the forward sweep and 24 bins on the backward sweep. Hence it follows that the centre producing the second peak in each direction must have lain in advance of its fellow by 3 bins (0·22°) on the forward sweep and by 4 bins (0·28°) on the backward sweep. This asymmetry was doubtless due to the finite dimensions of a bin although there could well have been some asymmetry of the receptive field organization as well. In both directions, therefore, the dark edge discharge centre must have been in advance of the light by about 0·25° (Fig. 2*B*). The dotted line across the histogram in Fig. 2*A* is a minimal estimate of the level of the background discharge.

Confirmation of the above conclusion was given by recording from the right eye the separate responses to single edges (Fig. 2*C*), both light (continuous line) and dark (dotted line), but once more with binocular conditioning as above. Fig. 2*C* has been prepared by superimposing the relevant portions of the two single edge histograms in Fig. 4. Even though the starting location of the single edges was the same in each case, Fig. 2*C* clearly shows the dark edge discharge (D) was in advance of the light (L) by 3 bins for each direction of stimulus movement. Since the dark edge discharges in Fig. 2 are obviously correlated with the test slit applied to the right eye, the discharge centres responsible for them must be components in the receptive field for that eye. These centres must ordinarily be subliminal, at least for the right eye, since they failed to produce a

discharge in the series illustrated in Fig. 1. Furthermore, it is clear that binocular conditioning provides a facilitatory action that is not present with monocular conditioning (cf. also Figs. 4 and 6).

Two of the three slit widths selected for Fig. 1 were those that gave the maximal and minimal discharge peaks for the forward sweep. These results are also in keeping with the above conclusions. At a slit width of 0·29° the discharge peak was maximal because at that width the two edges of the slit were closest to being simultaneously applied to their respective discharge centres whereas at 1·14° the light edge discharge was minimal because at that width the dark edge of the slit then lay within an inhibitory sideband (see below). The spatial relations of the slit edges in the two situations with respect to the excitatory and inhibitory components in the receptive field can be appreciated from Figs. 2*B* and 3*B* (cf. Bishop *et al.* 1971*b*).

Fig. 2*B* is a semi-diagrammatic representation of the excitatory complex, the continuous line rectangle (L) being the light edge discharge centre and the remaining rectangles the subliminal excitatory centres. For each direction of stimulus movement the dark edge centre (stippled rectangle) lies in advance of the light edge centre (open rectangle) such that the midpoints of the centres are separated in each case by 0·25°. Furthermore, the dark edge centre in one direction is spatially coincident with the light edge centre in the reverse direction. The lengths of the various centres in the direction of stimulus movement have been drawn to scale; the dimensions at right angles are arbitrary. Because of the relatively long bin duration (50 msec) it was not necessary to apply a correction for the latency of the responses (cf. Bishop *et al.* 1971*a*).

Inhibitory regions

Both monocular and binocular conditioning methods were used to reveal the inhibitory regions in the receptive field, the presence of inhibition being assessed with respect to the mean frequency of the background discharge. The level of this mean frequency can be estimated by operating the conditioning stimulus on its own as in Fig. 3*A*. In general, however, the best use of the available recording time was achieved by monitoring the background firing from records in which both conditioning and testing stimuli were operative. Wherever possible, the background firing level was estimated from spike counts in the 10 bins to either side of the turn-round point on the understanding that the testing stimulus was then completely outside the receptive field. In each histogram the background firing level is indicated by the upper border of the stippled band and it will be assumed that this level is equivalent to the discharge threshold for the testing stimulus. The warrant for this assumption is that, with monocular conditioning, the portion of the histogram above the mean level is nearly always

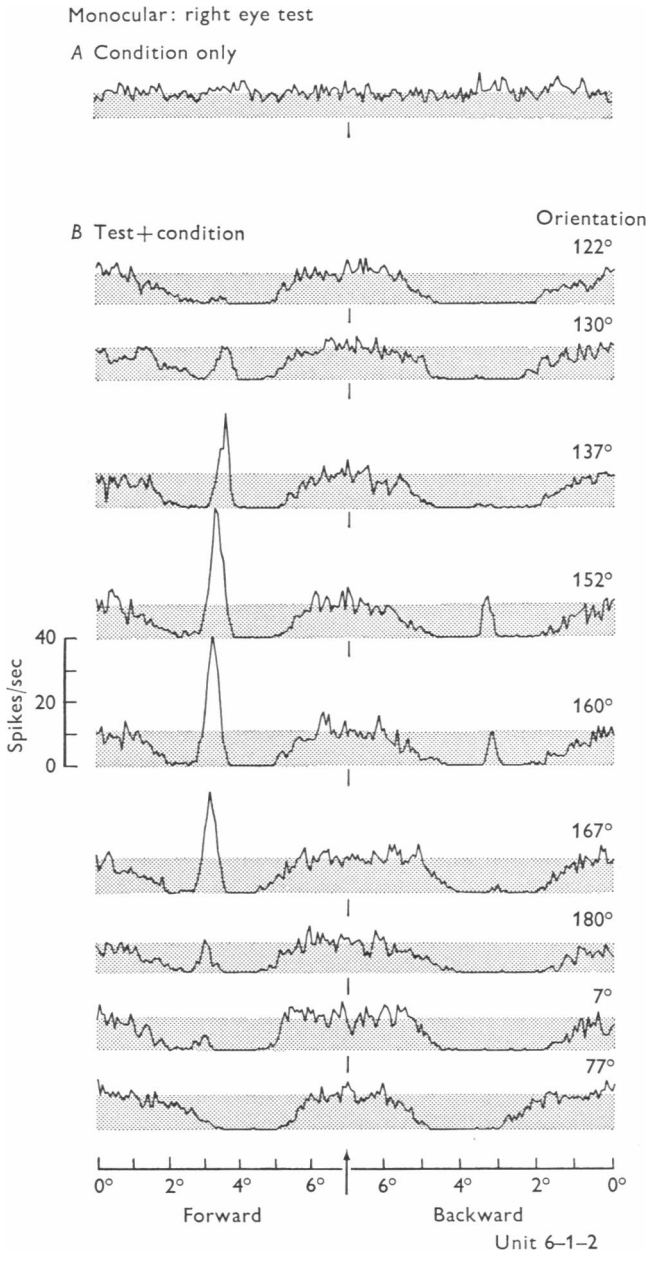

Fig. 3. For legend see facing page.

closely similar to the histogram produced by the testing stimulus in the absence of the conditioning stimulus. Thus we can compare Fig. 6*A* (R.E.). with the relevant portion of the histogram in Fig. 3*B* (152°). On this assumption, the normal 'resting' condition of the cell as far as the testing stimulus is concerned must be at a level somewhat below the mean level of the background discharge. Bin counts significantly above and below the mean level have, therefore, been taken to indicate firing to the testing stimulus on the one hand and inhibition on the other.

Inhibitory sidebands: monocular conditioning

The series of histograms in Fig. 3 were all obtained from the one cell (6–1–2) using monocular conditioning applied to the right eye (for details see legend), the unit being tested with an 0·29° slit angled over a wide range of different orientations. The orientation of the conditioning slit was kept constant at 167°, this being the initial estimate of the optimal orientation as determined by hand at the plotting table. The optimal orientation subsequently proved to be 156° (Fig. 5). At the outset the mean frequency of the background discharge was estimated by presenting the right eye with the conditioning stimulus on its own (Fig. 3*A*). Although the testing slit was shuttered during this procedure, its driving wave form continued to recycle the multichannel scaler (see Methods). The histogram was built up over the time taken for 50 cycles of the testing wave form. Over this time there were 275 cycles of the conditioning stimulus, each sweep producing an average of 13 spikes. For the histograms in Fig. 3*B* both the stimuli, conditioning and testing, were active, each of the histograms being obtained by summing the responses during 50 sweeps of the testing slit. The movements of the two slits were always broadside to their orientations. The histograms are a form of *activity profile* (Bishop *et al.* 1971*c*) representing the excitability of the cell at successive stages across the receptive field in the direction of stimulus motion.

When the slit orientation was close to optimal (156°; cf. Fig. 5), the histograms are marked on the forward sweep by a large discharge peak

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Fig. 3. Average response histograms using monocular conditioning to reveal inhibitory regions in the receptive field.

A, histogram of responses from the right eye to conditioning slit (2·9° × 0·29°; orientation 167°) on its own moving over a 1·1° traverse at 1·3°/sec and taken over 500 sec.

B, monocular conditioning as for *A* but with testing slit as well, the latter angled over a range of orientations as indicated. Testing slit (2·9° × 0·29°) moved at 1·4°/sec. Each histogram sums 50 sweeps of test stimulus using 200 analyser channels at 50 msec/bin. Upper border of stippled band in this and later Figures indicates the mean level of the background discharge.

flanked on both sides by deep inhibitory sidebands each about 2° across. For any given direction of slit movement we shall refer to the sidebands that lie before and after the discharge centre as being proximal and distal respectively and the inhibition will be regarded as complete when the bin count is reduced to zero. On the forward sweep at slit orientations near the optimal, the inhibition is complete over much of the distal sideband. On the backward sweep the spike discharge is replaced by a small 'peak' that barely rises above the mean level of the background discharge. We have already pointed out that, for unit 6–1–2, this peak represents a subliminal excitatory centre for the light edge of the slit. Once again there are, on the backsweep, inhibitory sidebands on both sides of this subliminal centre, the inhibition being even more intense here than on the forward sweep. In fact it is only because of the presence of the inhibition that the subliminal peak can be appreciated. On the forward sweep and to either side of the discharge peak, the transition from firing to deep inhibition is extremely rapid while towards the outer limits of the sidebands the firing returns much more gradually to the mean background level. When the testing slit was angled away from the optimal orientation, the amplitude both of the discharge peak on the forward sweep and the subliminal 'peak' on the backsweep rapidly declined and both were soon replaced by strong inhibition. The sequence of events for the two peaks were closely similar and the more profound inhibitory effect in the non-preferred direction of stimulus movement persisted even when the orientation became 90° to the optimal.

Inhibitory sidebands: binocular conditioning

Since cell 6–1–2 gave a nearly equal response from the two eyes (Fig. 6*A*), the results obtained by the techniques of monocular and binocular conditioning can be compared in the one cell. Using conditioning for the right eye and applying the testing stimulus to the left eye, a series of histograms was obtained over the same range of testing slit orientations as for Fig. 3. This series of histograms provided the data for Fig. 5*B* and two of the histograms are illustrated in Fig. 6*B*(II) (L.E.). A few histograms at different slit orientations were also obtained using the left eye for conditioning and the right eye for testing and two of these histograms are included in Fig. 6*B*(II) (R.E.). A direct comparison between the monocular and binocular conditioning methods can be made in Fig. 6*B* where it can be seen that there is a strong general similarity between the activity profiles obtained by the two methods. The differences between the two are that, with binocular conditioning, the excitatory responses are facilitated and the intensity of the inhibition is somewhat reduced. The facilitatory effect is particularly marked for the left eye where a very small

subliminal 'peak' on the backsweep of the monocular histogram is transformed by binocular facilitation into a clear discharge peak well above the mean level of the background discharge. The general form of the inhibitory sidebands remains the same, with the distal sideband on the forward sweep showing the greater inhibition. Once again, as in Fig. 3, the discharge peaks rapidly declined when the slit was angled away from the optimal orientation (cf. Fig. 5).

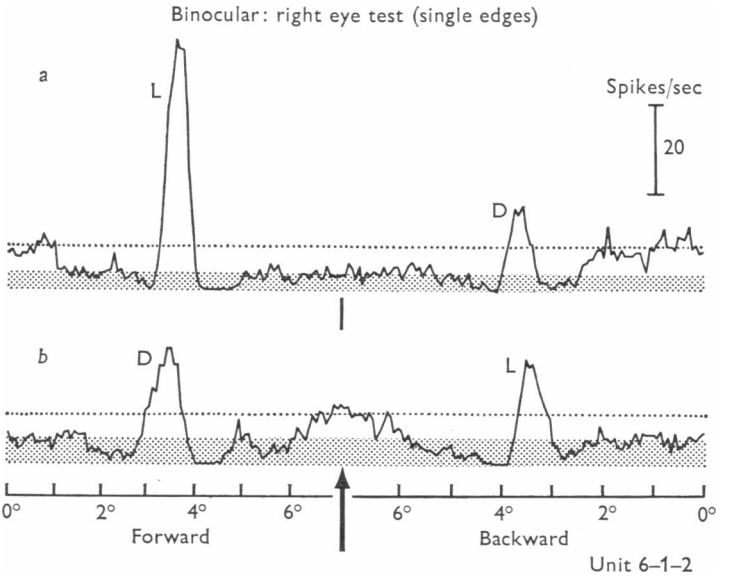

Fig. 4*a*, *b*. Activity profiles for right eye from cell 6–1–2 using binocular conditioning and testing with single optimally oriented light (L) and dark (D) edges, each edge being tested in both directions of stimulus movement. Binocular conditioning reveals three subliminal excitatory responses to single edges but shows that inhibitory regions lack stimulus specificity. Dotted line and upper margin of stippled band respectively indicate the mean level of the background discharge when the receptive field was in the darker and lighter regions to either side of the stimulating edge.

Inhibitory regions: responses to single edges

Since a single light or dark edge is the basic stimulus for simple cells, it is clearly essential to discover to what extent the inhibitory regions in the receptive field are specifically associated with one or other edge in a manner analogous to the excitatory centres. This problem will be taken up in detail in a later paper but some preliminary observations were made on cell 6–1–2. Fig. 4 shows the responses for the right eye to single light (L) and dark (D) edges moving in both directions using binocular conditioning to reveal the inhibitory regions. It should be recalled that a light edge on

the forward sweep becomes a dark edge on the backsweep and *vice versa* for the other edge. The sustained change in level of illumination that followed the passage of an edge altered the excitability of this cell so that the background discharge during the higher level of illumination fell to about 4 spikes/sec while at the lower light level it rose to about 12 spikes/sec. The dotted lines in Fig. 4 approximate the mean level of the background discharge under the darker conditions and the upper border of the stippled band gives the mean level under the lighter conditions. While similar changes in the background discharge have been seen in a number of cells, just as frequently the observation has been that changes in the steady illumination for one eye have little effect on the firing from the other eye.

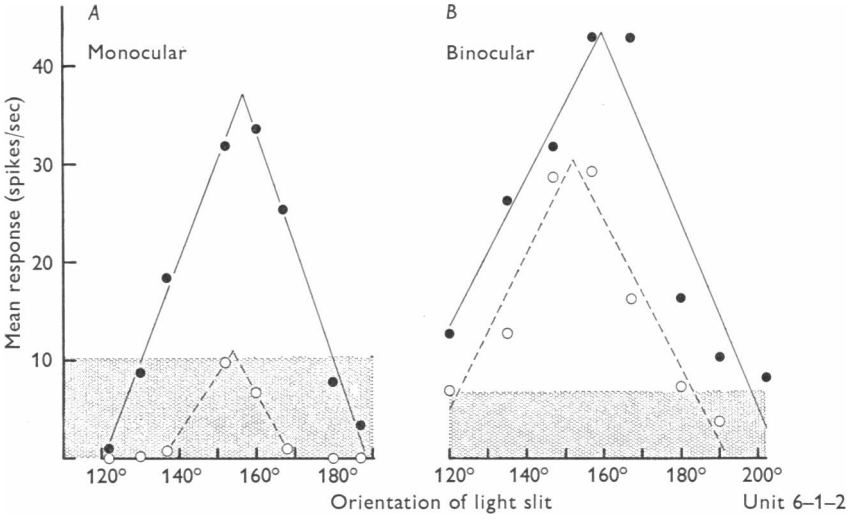

Fig. 5. Orientation specificity of excitatory components in the receptive field using monocular (*A*) and binocular (*B*) conditioning to reveal subliminal excitatory component (open circles). Filled circles: orientation specificity of discharge peak. *A*: right eye test; *B*: left eye test.

The change in excitability due to the shift in steady light level has to be distinguished from the inhibition directly due to the light and dark edges. With each type of edge, and in both directions of movement for each edge, the receptive field of cell 6–1–2 has inhibitory sidebands on either side of the four discharge centres. In addition, for each direction of movement, the form of the sidebands is the same whether the edge is light or dark. Just as for the narrow slit (Fig. 3), the inhibition is complete for the distal sideband on the forward sweep. Thus, the inhibition shows little specificity either for the type of edge or the direction of movement.

Orientation specificity

Details concerning the orientation specificity to a narrow slit on the part of the discharge centres of cell 6–1–2 are given in Fig. 5, the data for Fig. 5*A* being derived from Fig. 3. With monocular conditioning (*A*) the discharge peaks for the forward (filled circles) and the backward (open circles) directions are due to the light edge. With binocular conditioning (*B*), however, the peaks probably have a discharge component from both edges. Extrapolations of both the monocular and binocular curves give approximately the same orientation specificity, namely 156°, so that the

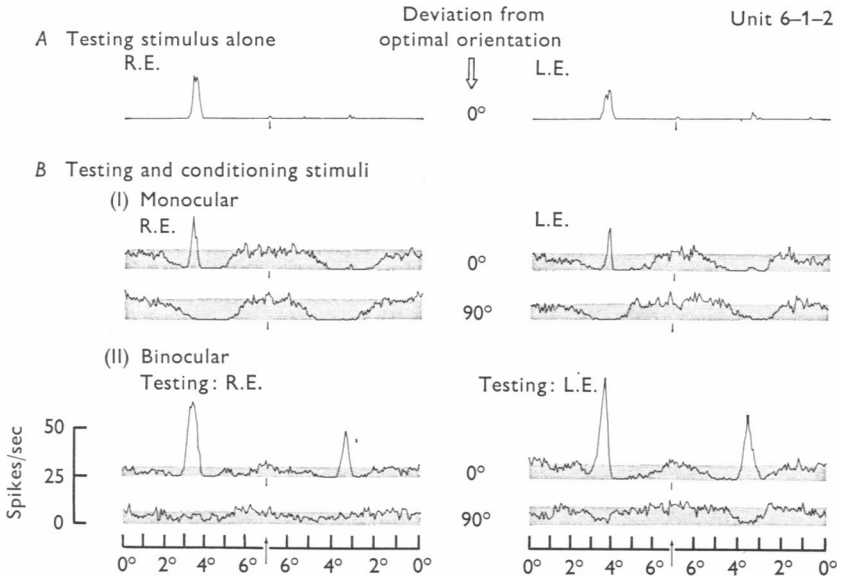

Fig. 6. Average response histograms from cell 6–1–2 to a narrow testing slit (2·9° × 0·29°) moving at 1·4°/sec showing the close similarity of the responses from the right eye (R.E.) and the left eye (L.E.) under a variety of stimulating conditions both without (*A*) and with (*B*) a background discharge (monocular and binocular) and with the testing slit at the optimal orientation and at 90° to the optimal. *A*: each histogram sums 20 stimulus sweeps. *B*: each histogram sums 50 testing stimulus sweeps.

specificity is the same not only for both directions of slit movement but also, in all probability, for the four discharge centres as well. The latter point would have been decided by the use of a wide slit which would have enabled the orientation specificity of each of the four discharge centres to be determined independently. Later work in this laboratory has confirmed that all the discharge centres of a given simple cell do, in fact, have the

same orientation specificity. The interesting point also emerges from Fig. 5 that the specificity is the same whether the centre is subliminal or supraliminal. For Fig. 5*A* the testing stimulus was applied to the right eye whereas for Fig. 5*B* the left eye was used. The graphs show that, despite the fact that different methods were used in each case, the two eyes have the same optimal stimulus orientation.

Comparison of test responses from the right and left eyes

While the ocular dominance of simple cells varies widely from cell to cell, there are, however, many cells, designated group 4 by Hubel & Wiesel (1962), that show 'no obvious difference in the effects exerted by the two eyes'. Cell 6–1–2 belonged to this group and Fig. 6 shows the remarkable similarity that can obtain between the receptive field organization for the two eyes. The similarity in this case is all the more remarkable when it is considered that the histograms used to make up this figure have been taken from various series recorded over many hours and involving a wide range of different stimulus parameters (for details see legend to Fig. 6). In this investigation, only one other cell (also group 4) was tested in a manner similar to 6–1–2 so as to allow a detailed comparison between the test responses from the two eyes. This cell also showed the same striking similarity between the responses from the two eyes. Such a close similarity between the receptive field organization for the two eyes may not always be the case, however, even when the discharges to a narrow slit are the same for each eye. As a result of studying binocular interaction fields Bishop *et al.* (1971*c*) concluded that when the inhibitory sidebands showed a monocular asymmetry there was likely to be an asymmetry between the two eyes as well.

PART 2

Unimodal simple cells: general properties

So far we have described the responses of a particular cell (6–1–2) in some detail. This cell, in addition to having inhibitory sidebands symmetrically arranged on either side of the discharge centre, was, in most other respects as well, typical of one of the commonest types of unimodal simple cell. Fig. 7 gives an impression of the various types of activity profile to be obtained from unimodal simple cells in response to the movement of an optimally oriented slit. Responses from three cells are illustrated, the upper histogram of each pair being without conditioning and the lower with monocular conditioning. Cell 16–2–4 had an unusually high rate of maintained (spontaneous) discharge (upper trace), had symmetrically arranged inhibitory sidebands and fired equally well to a slit moving in either direction. Cell 24–2–2 illustrates an activity profile with markedly

asymmetrical sidebands, the proximal band in this case being much shallower and less extensive than its fellow on the distal side of the discharge centre. The feature illustrated by cell 26–3–4 is the excitatory flank (indicated by the open arrow) that immediately precedes the proximal sideband. Excitatory flanks are regions of subliminal excitation or weak

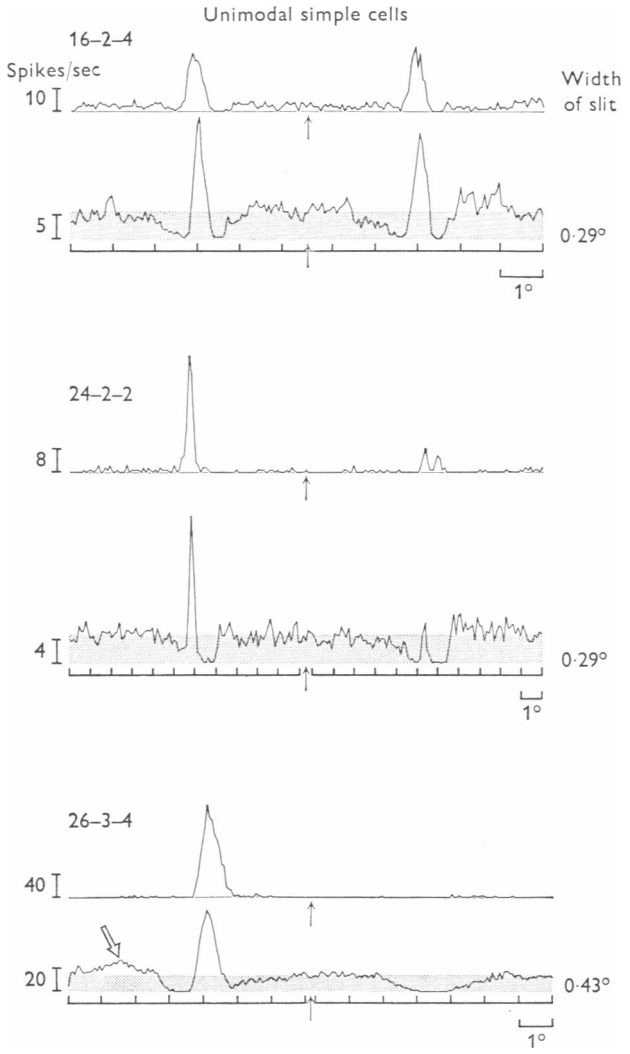

Fig. 7. Average response histograms from three unimodal simple striate cells showing types of activity profiles using, in each case, a narrow testing slit against the background of monocular conditioning. The upper histogram of each pair shows the response to the testing slit on its own and the lower histogram the response with conditioning. Open arrow: excitatory flank.

discharge that lie outside the peripheral margins of the inhibitory sidebands, either on one or both sides of the receptive field (Bishop *et al.* 1971*c*). Most commonly the excitatory flank is to be found only on one side of the receptive field and its excitatory action is usually subliminal. Thus, there is not usually any evidence of it in the average response histogram from a unimodal simple cell when only a narrow testing slit is used in the absence of any conditioning (Fig. 6*A*). Occasionally, however, there may be a frank discharge and it is possible to assemble a series of activity profiles from different cells having excitatory flanks of increasing amplitude over the series until the profile becomes indistinguishable from that typical of a bimodal simple cell. The two discharge centres in the receptive field of a bimodal cell are edge specific (Bishop *et al.* 1971*a*), one centre firing to a light edge and the other to a dark edge. Although a systematic analysis will need to be done, in the few cases where this point has been examined the excitatory flanks were also edge specific. The possible origin of excitatory flanks will be referred to in discussion.

Inhibitory sidebands of unimodal simple cells: general properties for narrow slits

Our earlier study of binocular interaction on simple cells (Bishop *et al.* 1971*c*) led to detailed predictions concerning the nature of the inhibitory sidebands, which have been fully confirmed in the present study. Every unimodal simple cell we have examined in sufficient detail with narrow moving slits had inhibitory sidebands on both sides of the discharge centre. Excluding unit 57–1–7 (Fig. 8), the present series of eighteen units with receptive fields within 3° of the visual axis provided twenty-three activity profiles using monocular conditioning. For two units, profiles were available for each of the two eyes and, in a further three units, there were profiles with discharge peaks in both directions of stimulus movement; i.e. the latter three units were not direction selective. The discharge centre averaged 0·6° across (range 0·17–1·26°), the larger sideband in each case averaged 2·0° across (range 0·6–4·8°) and for the smaller, the mean value was 1·3° (range 0·2–3·8°), the measurements being taken in the preferred direction of stimulus movement. Thus, the receptive fields as a whole averaged 3·9° across (range 1·7–9·5°). The width of the inhibitory region in the null direction of stimulus movement was 4·2° (range 1·6–10·5°). Only a relatively small number of units have been tested with the slit orientation at 90° to the optimal but the observations that we have made indicate that the receptive fields have an approximately circular shape. Thus, the mean width of the inhibitory region when the slit is at 90° to the optimal is probably close to 4°.

In the present series there was only one instance where the inhibition

was not complete (zero bin count) for at least one of the inhibitory sidebands and, even in this case, the background discharge was reduced by 90 % on both sides of the discharge centre. There was virtually complete inhibition (reduction > 90 %) on both sides of the discharge centre in the case of twelve of the twenty-three activity profiles. In the remaining eleven cases, on the incomplete side, the mean level of the background discharge was reduced on the average by 56 %. For any one unit, the proximal and distal sidebands may show marked differences but taking the series as a whole there were no statistically significant differences between the two groups of sidebands, proximal and distal, either in respect of form or potency. In the case of every activity profile which showed direction selectivity (seventeen profiles from fifteen units) the inhibition was always complete in the null direction of stimulus movement, the period of complete inhibition averaging 35 % (range 8–75 %) of the total duration of the inhibitory phase. In the case of 6 units, there was a subliminal peak in the inhibitory region for the null direction of slit movement. Two of these units had activity profiles plotted for both eyes and, in each case and for each eye, there was a subliminal peak for the null direction.

Plan representation of the reception field

An activity profile conveys only a limited aspect of the receptive field organization. A much more adequate idea is given by a plan representation such as that shown in Fig. 8 for unit 57–1–7. This plan has been built up from a series of thirteen activity profiles using monocular conditioning, and testing with a narrow slit moved over the receptive field. The rather large dimensions of the receptive field are to be attributed to its location, the centre of the field being about 5° from the visual axis. Six activity profiles were obtained with the slit at the optimal orientation (Fig. 8*C*, *D*), the cell firing in one direction of movement (*X*–*X*′) and being deeply inhibited in the reverse direction (*X*′–*X*). Between each recording the slit was offset by about half its length so that the responsiveness of the receptive field was sampled over a series of overlapping bands. The 7 activity profiles with the slit at 90° to the optimal (Fig. 8*E*, *F*) were obtained in a similar manner. The two activity profiles illustrated in Fig. 8*A*, *B* were obtained along the paths *X*–*X*′–*X* and *Y*–*Y*′–*Y* respectively. Both the activity profiles and the plan representations have been drawn to the same scale of visual angle but the slits are not to scale and are only diagrammatically located beyond the limits of their actual traverse. The discharge centre is represented in full black and the cross-hatched regions to either end of the centre are the two non-responding end zones (cf. Bishop *et al.* 1971*c*). These are regions which, for one direction of slit movement (*X*–*X*′), are without excitatory or inhibitory influence

on the background discharge. They are regarded as part of the receptive field not only because they are partially shut in by the inhibitory sidebands on the forward sweep, but also because, on the backsweep, they form an integral part of the total inhibitory field. Although it was not evident in this case, the parts of the end zones near the discharge centre are probably always regions of subliminal excitation so that the truly

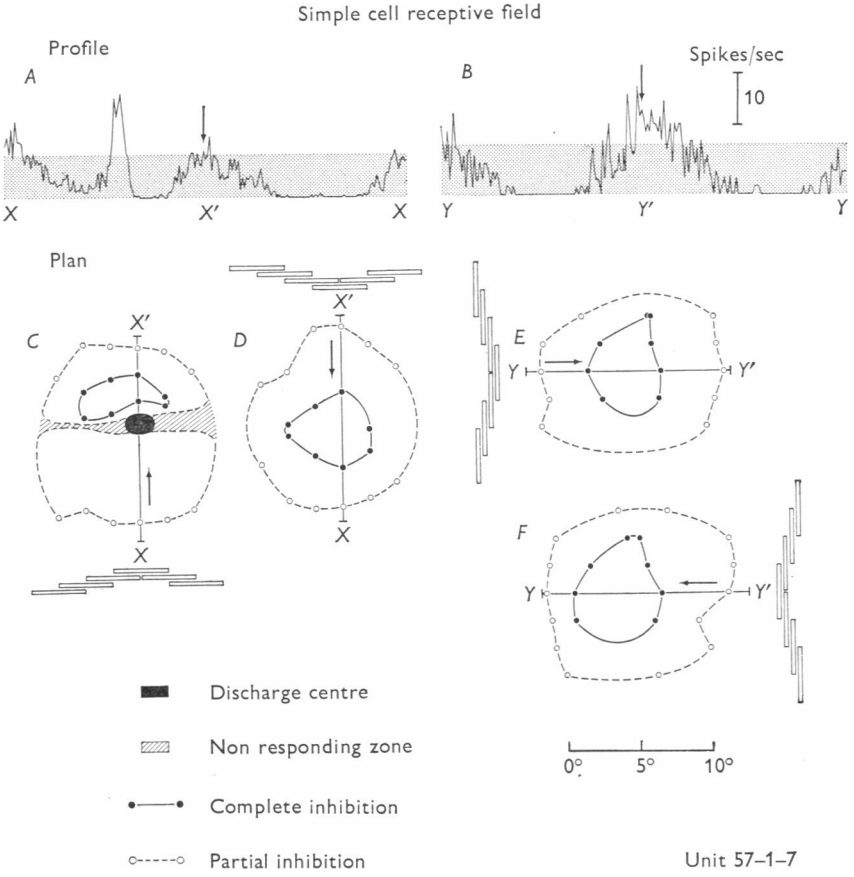

Fig. 8. Selected activity profiles (*A*, *B*) and plan representations (*C*, *D*, *E*, *F*) of the organization of a unimodal simple cell in response to a narrow slit (3·4° × 0·29°) moved forward and backward across the field at the optimal orientation (*A*, *C*, *D*–75°) and at 90° to the optimal orientation (*B*, *E*, *F*–165°). Profiles and plans are to the same scale but slits are not to scale and are only diagrammatically located in relation to the plans. Monocular conditioning was used and the testing slit moved over a 14·0° traverse at 11·3°/sec. The two activity profiles (*A*, *B*) were obtained over the traverses X–X'–X and Y–Y'–Y respectively as shown in *C*, *D*, *E* and *F*. Receptive field 5° from visual axis.

non-responding parts of the end zones may be quite small or even absent. The lines joining the filled circles enclose regions of complete inhibition while between the continuous and dashed lines lie regions where the cell was only partially inhibited. Although this receptive field was one of the largest in the present series, the relative sizes of the various regions in the field were approximately the same as those of the much smaller receptive fields. The plan representation in Fig. 8 brings out very clearly the dominant nature of the inhibitory components and their relative non-specificity as to stimulus requirements in contrast to the comparatively small size and precise stimulus specificities of the discharge centre. The term 'inhibitory sideband' is obviously appropriate when an optimally oriented slit is moved in the preferred direction but Fig. 8 also makes it clear that the spatial distribution of the inhibition is really saucer-shaped, encompassing the whole receptive field and only momentarily relieved by the optimal stimulus.

DISCUSSION

We can now relate our concepts of cortical subliminal excitatory and discharge centres to the properties of the geniculo-cortical input, discuss the nature of the mechanisms reponsible for sideband inhibition and, finally, attempt to reconcile the cortical receptive fields mapped with stationary flashing lights with those plotted by moving stimuli.

Excitation

Two obvious possibilities suggest themselves as a basis for the excitatory complex.

(1) Each type of discharge centre could result from a separate geniculo-cortical input either from a single lateral geniculate neurone or, more probably, from a group of neurones having receptive fields arranged along a line. Thus a light edge centre could have as input a row of ON centre geniculate cells and a dark edge centre a row of OFF centre cells. This double row concept was part of our earlier receptive field model (Bishop *et al.* 1971*b*).

(2) The two types of discharge centre could represent different response components from the one geniculo-cortical input. Thus the light edge and dark edge centres could be identified with the centre and surround components either of a single geniculate receptive field or a single row of fields. The evidence now available supports a single row concept.

We have shown (Bishop *et al.* 1971*a*) that, when simple cells are stimulated by single edges moving in one direction, the most common arrangement of discharge centres is for the dark edge centre to be about 0·3° nearer the starting point of movement than the light edge centre and that,

when the cell responds to both directions of stimulus motion, the dark edge centre in one direction occupies approximately the same location in space as the light edge centre in the reverse direction. The analysis by Dreher & Sanderson (1973) of the responses of lateral geniculate neurones both to extended single light and dark edges and to narrow slits indicates

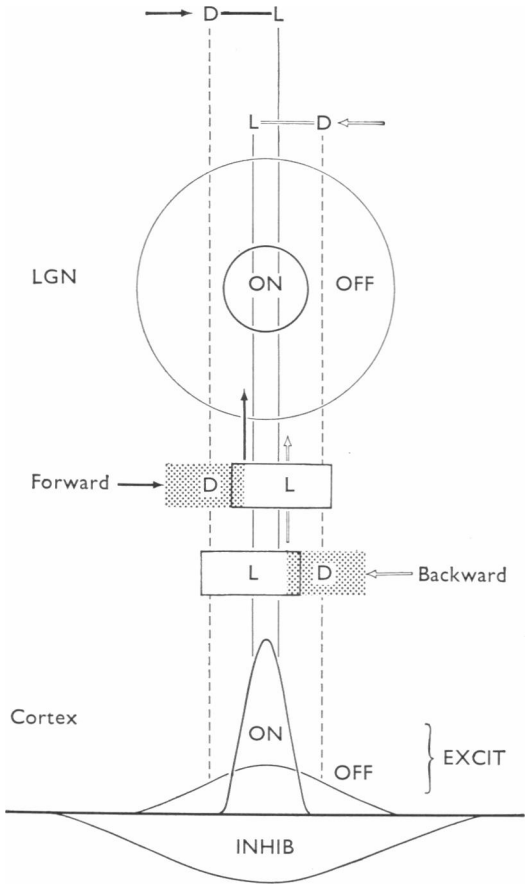

Fig. 9. Diagram showing the relationship of the excitatory (EXCIT – ON, OFF) and inhibitory (INHIB) components in the receptive field of a simple cortical cell to the ON centre and OFF surround receptive field components of a geniculate neurone. Vertical lines: regions from which peak firing is obtained to the movement of single light (L – continuous lines) and dark (D – interrupted lines) edges in the forward (horizontal filled arrow) and backward (horizontal open arrow) directions. Open and stippled rectangles illustrate the concept of discharge 'centres' for light and dark edges respectively. Vertical arrows: regions of peak firing to the movement of narrow slits in the forward (filled arrow) and backward (open arrow) directions.

that most, if not all, of the firing patterns of simple cells in the cortex can be accounted for on the basis of an excitatory drive from a single row of geniculate receptive fields.

Consider first geniculate cell firing to *single edges*. Fig. 9 diagrams the usual responses to light (L) and dark (D) edges (and to narrow slits) by geniculate cells with an ON centre, OFF surround receptive field. The continuous and dashed vertical lines respectively indicate the positions for peak firing to the light and dark edges when each is separately moved forward (horizontal filled arrow) and backward (horizontal open arrow) across the field. Consider first movement in one direction. A small dark edge discharge comes from the first part of the OFF surround (proximal part) and a much larger light edge discharge comes from the ON centre. In addition there is commonly a very weak dark edge discharge from the distal part of the OFF surround. This last peak has been neglected in Fig. 9 because, being much smaller than the dark edge discharge from the proximal surround, it would, in all probability, be suppressed by cortical inhibition (see below). The above firing patterns to single edges are diagrammatically represented in terms of discharge 'centres' by the rectangles located below the geniculate receptive field in Fig. 9, the dark edge centre (D) being stippled and the light edge centre (L) being open.

When both directions of edge motion are considered it can be seen that the dark edge discharge still precedes the light edge discharge and that the spatial locations of the centres in the one direction are approximately the reverse of those in the other direction. This reversal at the geniculate level is essentially identical with that seen in many cortical fields. It indicates that the simple cells with this type of field receive input from a single row of ON centre geniculate cells (possibility 2 above), and that the cortical fields are not formed by two rows of geniculate receptive field centres, one ON and the other OFF (possibility 1 above), since in this case no reversal should be apparent.

The main peak of firing by geniculate cells always comes from the centre component in the receptive field. The subsidiary peaks that come from the receptive field surround, being frequently of small amplitude, would be readily blocked at the cortical level by the marked tonic and sideband inhibitions that seem to be a feature of the simple cell input (see below). Thus, even simple cells, that respond to only one kind of edge and then only in one direction of motion (e.g. cell 6–1–2 above), may, nevertheless, receive subliminal inputs from the geniculate cells in response to the other edge in the preferred direction and to both edges in the null direction. With appropriate binocular stimulation it is indeed possible to reveal inputs from the geniculate that are normally only subliminal. Thus, we found cell 6–1–2 to have subliminal 'excitatory centres' that were arranged

in a manner entirely compatible with the idea that this cortical cell had an excitatory drive from a single row of ON centre geniculate neurones. Furthermore, it is worth noting that the centre size of the geniculate receptive fields near the visual axis (about 0·4° diameter; Dreher & Sanderson, 1973) is clearly compatible with the spatial separation of the discharge centres in the simple cell receptive fields.

The response patterns of OFF centre geniculate cells are nearly mirror images of those from ON centre cells (Dreher & Sanderson, submitted for publication; they are in keeping with the idea that simple cells having the reverse spatial arrangement of discharge centres, namely light in advance of dark, might have as input a row of OFF centre geniculate cells. However, OFF centre geniculate cells show rather more variability in their response patterns than do ON centre cells. Furthermore, though the two types of geniculate cells have receptive fields of about the same size, the discharge peaks from OFF centre cells are significantly further apart than are those from ON centre cells, the peaks being sufficiently separate in a number of cases to account for the spatial arrangement of the discharge centres of the bimodal type of simple cortical cell. All the bimodal simple cells have the light edge discharge centre in advance of, and clearly separated from, the dark edge discharge centre (Bishop *et al.* 1971*a*). Furthermore, there are geniculate discharge patterns that can satisfactorily account for some, at least, of the multimodal type of simple cell discharge patterns. There are indeed so many clear-cut parallels between the discharge patterns of geniculate cells and those of simple cells that it is highly probable that all the various types of simple cell, unimodal, bimodal and multimodal, each have as input a single row of geniculate receptive fields, the row being either all ON centre or all OFF centre.

For those simple cells that respond in both directions of stimulus motion, the spatial arrangement of discharge centres in one direction is, however, not always the reverse of that in the other (Bishop *et al.* 1971*a*). There is indeed a variety of spatial arrangements. Further work is needed to decide the extent to which these less common arrangements can still be explained on the basis of a single row of geniculate cells or whether it will be necessary to invoke the idea of a partially overlapping double row of geniculate cells with ON centre cells in one row and OFF centre cells in the other. It is probable that the excitatory flanks in the cortical receptive fields represent subsidiary peaks in the geniculate discharge which are ordinarily subliminal at the cortical level.

So far we have considered geniculate cell responses to single edges but when *narrow slits* are used rather different firing patterns emerge and the responses can no longer be ascribed to one or other edge. With ON centre cells, a single very narrow peak of firing dominates the response in each

direction of slit motion, the locations at which the peaks occur being indicated in Fig. 9 by the vertical filled and open arrows. The peaks tend to occur between the two positions at which maximum firing is obtained to single light and dark edges. Furthermore, the first peak in the single edge response that comes from the proximal part of the OFF surround tends to disappear and a small peak associated with departure of the slit from the distal part of the OFF surround now makes an appearance. However, the latter peak presumably fails to reach the firing level for the cortical cell because the usual response to a narrow slit is a single narrow peak, i.e. a unimodal response. This would explain why simple cells having two slightly offset single edge discharge centres, nevertheless, respond to narrow slits with a single sharp peak whose duration is rather briefer than would be suggested from a combination of the action of the two discharge centres. Furthermore, this single peak tends to lie between the two single edge discharge peaks.

Inhibition

Simple cells are possibly subjected to two kinds of inhibitory action, namely *tonic inhibition* and *sideband inhibition*. There is no clear distinction between the two inhibitions and both probably operate through the same intra-cortical mechanisms. We suggest that tonic inhibition is due to the normal maintained discharge of geniculate neurones which occurs under resting conditions and in the absence of retinal stimulation. Sideband inhibition, on the other hand, is a component of the cortical cell receptive field organization that is made manifest by photic stimulation of the retina, and especially by moving stimuli. The term 'sideband' is somewhat unsatisfactory because, for non-optimal stimuli, the whole receptive field becomes inhibitory so that the sideband regions then merge into the one roughly circular area encompassing and surrounding the area that had been excitatory. Thus the inhibitory component (INHIB) in Fig. 9 includes and extends beyond the excitatory (EXCIT) components (ON and OFF) (cf. Bishop, Dreher & Henry, 1972). We have already suggested (Bishop *et al.* 1971*b*) that all the geniculo-cortical afferents are excitatory and that inhibition is applied to the simple cells via intra-cortical interneurones. We have further suggested that the cortical cells which lack orientation specificity have all the properties that would fit them for the role of the inhibitory interneurones.

If, as we have concluded above, simple cells receive an excitatory drive from a single row of geniculate cells, either all ON centre or all OFF centre, then the geniculate receptive field surround components would form two bands, one on either side of the line of geniculate centres. What then is the relationship of these geniculate surrounds to our concept of

inhibitory sidebands at the cortical level? Both the geniculate centre and surround components lead to excitation of the cortical cell (Fig. 9). Hence, if the geniculate surrounds generate the inhibitory sidebands, they can do so only by inhibition supplied at the geniculate level; i.e. by inhibiting the centre component. This possibility as a basis for sideband inhibition appears to be excluded by the fact that the centre and surround components interact reciprocally in respect to excitation and inhibition. Thus, any inhibition of the centre by the surround must necessarily be accompanied by excitation of the surround. In addition, this inhibitory action is edge specific in that only the type of edge that excites the centre component would be rendered ineffective. This type of inhibitory response pattern is markedly different from that given by the inhibitory sidebands. Except perhaps for stimulus movement (see below), the sidebands are not at all stimulus specific, whether for edges, slits or bars, and their influence appears to be purely inhibitory. Thus, while the geniculate surround components undoubtedly contribute to both excitatory and inhibitory phenomena at the cortical level they cannot be the major element responsible for sideband inhibition. Similarly, the geniculate suppressive field (Levick, Cleland & Dubin, 1972) can play only a minor part in the production of sideband inhibition. The suppressive field is purely inhibitory and must therefore have its action by opposing geniculate excitation. Furthermore, it has only a small effect in reducing the geniculate responses to long narrow slits or edges whereas sideband inhibition can completely suppress the cortical responses to the same stimuli.

There is, however, a further and compelling argument for regarding sideband inhibition as being due to an intracortical mechanism rather than a reduction in excitation at the geniculate or retinal levels, namely the fact that an inhibitory action from one eye can prevent the discharge from the other eye. While inhibitory binocular interaction does occur at the geniculate level (Sanderson, Bishop & Darian-Smith, 1971; Sanderson, Darian-Smith & Bishop, 1969; Singer, 1970) the effect is relatively weak, particularly in relation to the driven discharge. By contrast, binocular inhibition at the cortical level is extremely powerful (Bishop *et al.* 1971*c*), an inhibitory input from one eye being enough to eliminate completely the discharge produced by the other eye. The spatial distribution of the inhibitory sidebands as determined by binocular methods is the same as that obtained by monocular methods and once again the inhibition is not at all stimulus specific. Hence, it is highly probable that the monocularly established inhibitory sidebands are the same as those obtained by binocular methods. We may conclude, therefore, that sideband inhibition is due to an intracortical mechanism and that reduction of excitation at the geniculate level makes little, if any, contribution.

The striking parallels that exist between the firing patterns of geniculate cells (Dreher & Sanderson, submitted for publication) and those of simple cells (Bishop *et al.* 1971*a*) suggest that the cortical cells have a direct, and probably monosynaptic, drive from the geniculate level. This conclusion is strongly supported on other grounds by both histological (Colonnier & Rossignol, 1969; Jones & Powell, 1970; Garey & Powell, 1971) and electrophysiological (Hoffmann & Stone, 1971) evidence. Furthermore, there is strong independent evidence for the kind of intracortical inhibitory mechanism that is needed as a basis for sideband inhibition. Both histological (Jones & Powell, 1970; Szentágothai, 1971; Garey & Powell, 1971) and electrophysiological (Watanabe, Konishi & Creutzfeldt, 1966; Toyama & Matsunami, 1968) observations indicate that inhibition appearing at the cortical level is generated through cortical interneurones.

Comparison of responses to stationary and moving stimuli

The original definition of a simple cell (Hubel & Wiesel, 1962) was based on the observation that its receptive field could be mapped into spatially distinct ON and OFF areas that suggested to Hubel & Wiesel a model based on a row of concentrically organized geniculate receptive fields and we subsequently preserved this idea in a modified form in the model that we proposed (Bishop *et al.* 1971*b*). A major problem in our understanding of the organization of simple cell receptive fields has, however, been our inability to reconcile the maps produced by stationary flashing slits and those produced by moving stimuli (Bishop *et al.* 1971*a*; Henry & Bishop, 1972). Our analysis above has now revealed the true nature of this problem and shows the way to a satisfactory solution. This analysis has enabled us to dissociate those properties of the simple cell receptive field that are determined at geniculate level from those that arise as a result of mechanisms intrinsic to the cortex.

The responses of geniculate cells to stationary flashing stimuli reveal what may be called the *static* properties of the geniculate receptive fields in contradistinction to the *dynamic* properties of the same fields that are revealed by moving stimuli. The relationship between the static and dynamic properties of geniculate receptive fields are described in detail elsewhere (Dreher & Sanderson, submitted for publication; cf. also Rodieck & Stone, 1965*a*, *b*; Rodieck, 1965 for a similar analysis of retinal ganglion cells). As we have already pointed out, the responses to moving slits may differ considerably from those to single edges. Nevertheless, in large measure, it is possible to predict the dynamic properties of the geniculate receptive fields from a knowledge of the static properties. We now propose that the cortical maps produced by stationary flashing stimuli largely reflect the static properties of a line of geniculate receptive fields. The relatively simple static pattern

of elongated ON and OFF areas is, however, distorted at the cortical level by the presence of both tonic and sideband inhibition. Separate ON or OFF components of the geniculo-cortical input, or even the whole of the input, may be suppressed by the tonic cortical inhibition so that a discharge appears only when the slits or edges are moved. We have already suggested that moving stimuli produce enhanced firing from simple cells by a disinhibition mechanism (Bishop *et al.* 1971*b*) and recent work (G. H. Henry, P. O. Bishop & B. Dreher, unpublished observations) indicates that sideband inhibition is also enhanced by the movement of stimuli that are otherwise non-specific. Thus, all the intracortical mechanisms appear to respond much more vigorously to moving than to stationary stimuli. The above observations explain why the maps produced by stationary flashing stimuli not infrequently cover a much greater area than does the discharge centre as revealed by moving stimuli (Bishop *et al.* 1972). In other words, some regions may fire, even if weakly, to stationary stimuli and give only an inhibitory response to the same stimuli when they are moved. The observations also explain why some cells, whose responses to moving stimuli are, in every way, characteristic of simple cells, yet fail to respond to stationary stimuli. Since, on this view, it is largely the strength of the tonic inhibition which determines whether, and to what extent, the cells respond to stationary flashing lights, the term 'simple' could still be applied to the cells even though their receptive fields cannot be mapped into antagonistic ON and OFF areas.

When the slits or edges are moved the geniculo-cortical input is then determined by the dynamic properties of the geniculate receptive fields, again modified, of course, by intracortical mechanisms which become operative, or more fully so, only when the stimuli are moving. It is not surprising, therefore, that the receptive field maps produced by moving stimuli differ quite markedly from those obtained by stationary stimuli. If this analysis is correct, it explains why it is not possible to predict the responses of simple cells to moving stimuli from the maps of ON and OFF firing to stationary stimuli. Furthermore, it makes clear that the definition of simple cells is best made in terms of responses to moving stimuli since they are much more significantly determined by cortical mechanisms than those to stationary stimuli.

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