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QUANTITATIVE STUDIES OF ENHANCEMENT AND SUPPRESSION ZONES IN THE RECEPTIVE FIELD OF SIMPLE CELLS IN CAT STRIATE CORTEX

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SUMMARY

1. The configuration and extension of enhancement and suppression zones were compared with the configuration and extension of on- and off-response zones across the receptive field of simple cells in cat striate cortex. The enhancement and suppression zones were determined by a dual-stimulus technique where a stationary flashing light slit produced activity against which activation profiles across the receptive field were plotted with a parallel stationary test slit.

2. The activation profiles showed less variation in receptive field configuration than plots of on- and off-discharge zones. Whereas the number of on- and off-zones varied between one and five, the activation profiles showed at least three distinct subregions in the receptive field, i.e. a central zone with an adjacent oppositely responding zone on each side. The responsivity was clearly stronger in one of these proximal flank zones. An additional zone occurred distal to the strong proximal flank zone in 53% of the cells, and in 10% such a distal zone occurred distal to both proximal flank zones.

3. There was good correspondence between the location of on- and off-discharge zones and the location of the enhancement and suppression regions, although some subregions seen in the activation profiles did not appear in plots made with a single slit. The maximum discharge and the maximum enhancement and suppression effects in a subregion were found at the same receptive field location.

4. The width of a subregion was measured as the width of the eventual on- or off-discharge zone determined with a single slit, as the width of the enhancement zone, and as the width of the suppression zone determined with the dual-slit technique. The enhancement zone was narrower, and the suppression zone wider than the discharge zone. The strong proximal flank zone had the same width as the central zone, but was wider than the weak proximal flank zone. For most cells the distances between successive extreme points across the activation profiles were constant, and this may explain the selectivity of the cells for spatial frequency of periodic stimuli.

5. The strongest flank suppression occurred for most cells in that of the two proximal flank zones which had the strongest discharge to the single slit. Nevertheless, there was no correlation between the degree of discharge and the degree of suppression

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produced by opposite light cycles. This indicated that the location of the discharge and the location of the suppression were determined by a common restricting factor, but that the degree of discharge and the degree of suppression were determined by different factors.

INTRODUCTION

The on- and off-zones in the discharge field of simple cells are mutually antagonistic (Hubel & Wiesel, 1962). Hence, the discharge elicited from an on-zone is suppressed by simultaneous on-stimulation of an adjacent off-zone, and the discharge elicited from an off-zone is suppressed by simultaneous off-stimulation of an adjacent on-zone. Because of this antagonism Hubel & Wiesel (1962) termed the on-response excitatory and the off-response inhibitory. This could imply that an off-response zone shows the location, extension and relative strength of the on-suppression, but this has not yet been verified experimentally. Creutzfeldt & Ito (1968) showed by intracellular recordings from cat striate cortex cells that strong inhibition can occur in receptive field positions where a single stationary stimulus elicits no discharge. Also, from extracellular studies where suppression zones in the receptive field were plotted it has been reported that suppression can occur in zones where a single slit elicits no discharge (Bishop, Dreher & Henry, 1973; Heggelund, 1981; Palmer & Davis, 1981). This indicates that there is no direct relationship between on-suppression and off-discharge.

In the preceding paper (Heggelund, 1986) the configuration and extension of on- and off-discharge zones were analysed on the basis of data obtained with a stationary flashing light slit. Subregions of the receptive field can also be determined by techniques which involve an artificial increase of the cells' response level (Henry, Bishop & Coombs, 1969; Sillito, 1979; Heggelund, 1981). Such techniques are more sensitive for differences in receptive field configurations since they also reveal subliminal receptive field regions.

In the present study a static dual-stimulus technique (Heggelund, 1981) was used to make activation profiles across the receptive field. The configuration, location and extension of enhancement and suppression zones in these profiles were compared with the properties of on- and off-zones in discharge field plots made with a single slit. Furthermore, the degree of discharge (on- or off-response) and the degree of suppression produced by opposite light cycles in a given receptive field position were correlated. The results showed close overlap of receptive field zones where opposite light cycles produced discharge and suppression, but there was no correlation between the degree of discharge and degree of suppression in a subregion. The activation profiles showed considerably less variation in receptive field configuration than the discharge field plots.

METHODS

The general methods were described in the preceding paper (Heggelund, 1986). The quantitative receptive field analyses were made with a computer-controlled light projector which could present two light slits on a tangent screen in front of the cat. The dimensions and luminance of the two slits were the same. The slit parameters were selected so that a good response from the cell was elicited. Slit length varied between 0·7 and 10 deg, and slit width between 0·1 and 0·3 deg. The slit luminance was 0·3–1·0 log unit above the background which was about 5 cd/m.

First, the optimum stimulus orientation of the cell was determined from an orientation tuning curve made with a moving light slit. Secondly, static discharge field plot and static activation profiles were determined (Heggelund, 1981). An optimum oriented light slit (*activation slit*) was flashed on and off in the most responsive position of the discharge field, to produce activity against which the effect of a second parallel slit (*test slit*) could be measured. The test slit was flashed in a series of broadside positions across the receptive field. In each position the test slit was first flashed on and off alone. These data were used for the static discharge field plot which showed the distribution of on- and off-response across the receptive field. Then the test and activation slits were flashed on and off simultaneously. These data were used to make an activation profile which showed how the test slit in the various positions modified the response to the activation slit when the two stimuli were flashed *in phase*. Next, the test slit was turned off when the activation slit was turned on for on-dominant cells, and vice versa for off-dominant cells. An activation profile which showed how the test slit modified the response to the activation slit when the stimuli were flashed *in counterphase* was plotted from these data. Finally, the activation slit was flashed on and off alone. This sequence of stimulus conditions was only presented once in a test slit position before proceeding to the next position. When all positions were tested through once, the series of measurements was repeated. The number of repetitions varied from cell to cell between ten and fifty depending on the response variability and on how long the cell could be held. In this way the discharge field plot and the activation profiles were made in an interleaved manner to avoid discrepancies due to fluctuations in the responsivity of the cell.

The time window for the on- and off-periods was the same in all stimulus conditions for a cell, but varied from cell to cell between 0·5 and 1·0 s. For each stimulus condition and each test slit position a peristimulus–time histogram was determined. The cell responses were calculated from these histograms as the average firing rate during the on- or the off-periods. Enhancement was defined as response increase in the dual-slit conditions above the response to the activation slit alone. Suppression was defined as response reduction below the response to the activation slit alone.

Several width parameters of the activation profiles were measured. The values of the parameters increased with receptive field eccentricity, and paracentral fields looked like magnified central fields (Heggelund, 1986). For several of the parameters the sample of cells was too small to permit a reliable estimate of the values at the various eccentricities. The parameter values were therefore expressed relative to the width of the most responsive zone in the static discharge field plot (the *dominant discharge zone*). The variation of this parameter with eccentricity was presented in the previous paper (Heggelund, 1986), and those data can be used to estimate width values of the various parameters of the activation profiles at different eccentricities.

RESULTS

Data from ninety-four simple cells which had their receptive fields centred within 10 deg from the visual axes were analysed. Static discharge field plot and static activation profiles were obtained from all cells.

Receptive field configuration

The activation profiles revealed a higher number of subregions in the receptive field than the discharge field plots for most cells. Whereas the number of discharge zones varied from cell to cell between one and five (Heggelund, 1986) the number of subzones in the activation profiles varied between three and five, indicating that the receptive field organization among simple cells varies less than the discharge field plots indicate.

The response type in a subzone was opposite to that evoked in adjacent zones, e.g. if enhancement occurred in a zone the same stimulus would produce suppression in an adjacent zone. For ninety-one cells (97 %) at least three distinct subregions were revealed by the activation profiles, i.e. a central zone with an adjacent flank zone on each side (Fig. 1*B–C*). When the test and activation slits were flashed on or off

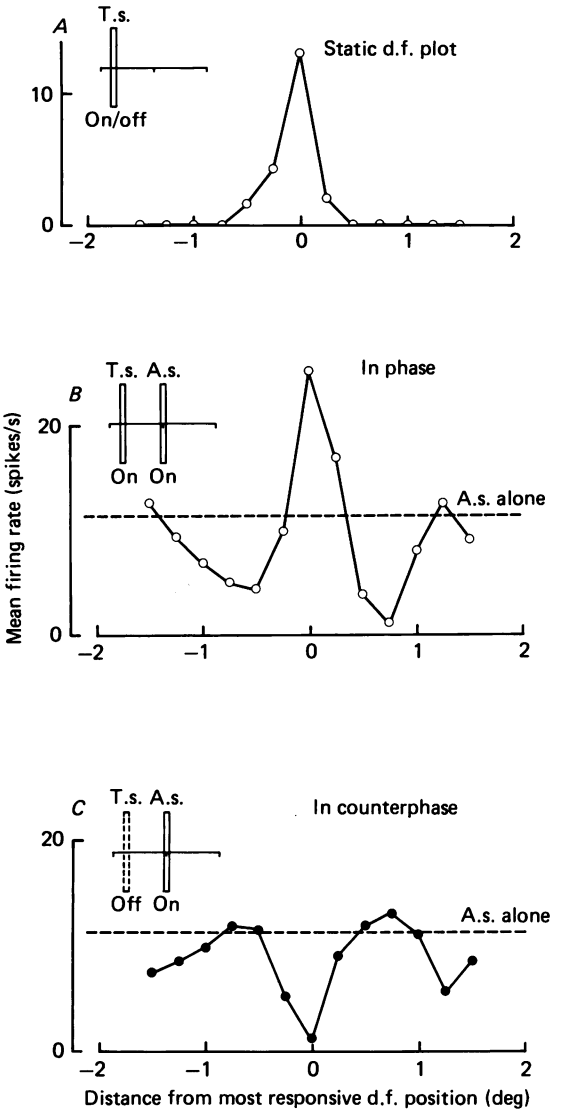

Fig. 1. Response profiles across the receptive field for an on-dominant S1 cell. The inset in each diagram illustrates the stimulus condition which was used. *A*, plot of the discharge to a single light slit which was flashed on and off in various broadside positions of the receptive field (static discharge field plot). The on- and off-periods were both 500 ms. The ordinates show the average firing rate during the on-periods. The abscissae show the distance from the position of the test slit to the position where the slit elicited the strongest response. *B*, static activation profile made by flashing an activation slit and a test slit in phase (both on simultaneously). The dashed horizontal line shows the response to the activation slit alone. Response above this level was defined as enhancement and response below this level as suppression. *C*, activation profile showing the response when the two slits were flashed in counterphase (test-slit off and activation slit on). The measurements were repeated 20 times for each t.s. position. The slit width was 0·2 deg, slit length 3·2 deg. Abbreviations in this and other Figures: d.f., discharge field; a.s., activation slit; t.s., test slit.

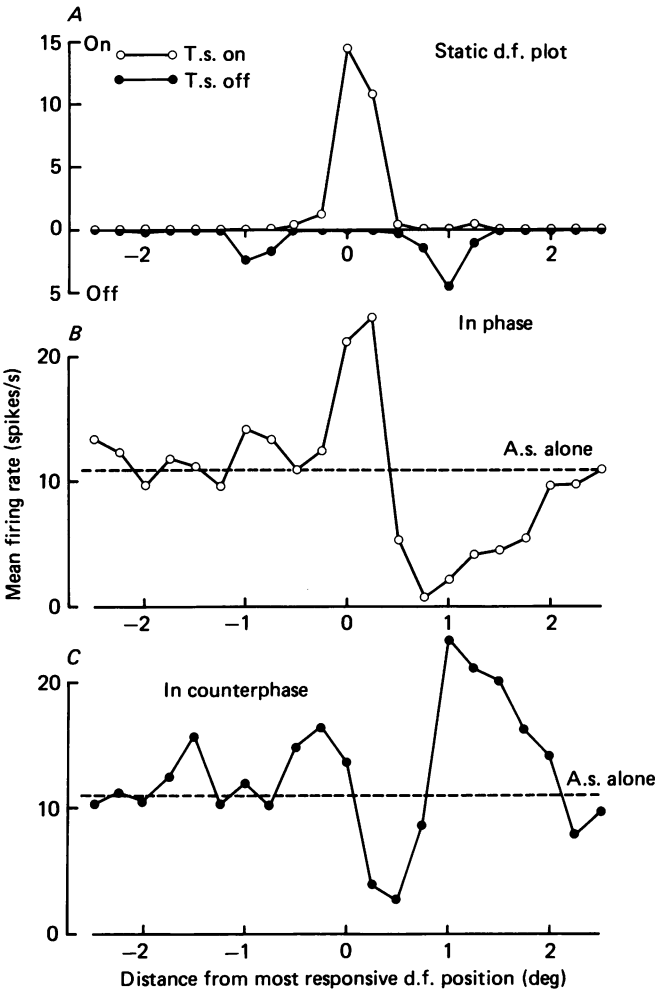

Fig. 2. Response profiles across the receptive field for an on-dominant simple cell. *A*, static discharge field plot made with an optimum oriented flashing light slit. ○, discharge to slit on; ●, discharge to slit off. *B*, static activation profile determined by double-slit experiments where test and activation slits were flashed on in phase. The dashed horizontal line shows the on-response to the activation slit alone. *C*, static activation profile showing the response when the test and activation slits were flashed in counterphase (a.s. on, t.s. off). The on- and off-periods were 500 ms, and fourteen measurements were made in each position. The slit dimensions were 6·0 × 0·17 deg.

simultaneously (in phase) enhancement was usually found in the central zone and strong suppression in the adjacent flank zones (Fig. 1 *B*). The suppression was always stronger on one side and the zones were accordingly termed the *strong* and *weak flank zone*. When the two slits were flashed in counterphase (test slit on and activation slit off, or vice versa) the opposite response pattern occurred (Fig. 1 *C*). All the cells which had only one discharge zone in the discharge field plot (S1 cells, $n = 6$), had these three subregions. An example is shown in Fig. 1. Notice the weak enhancement on both flanks (Fig. 1 *C*) although the single slit produced no discharge there (Fig. 1 *A*).

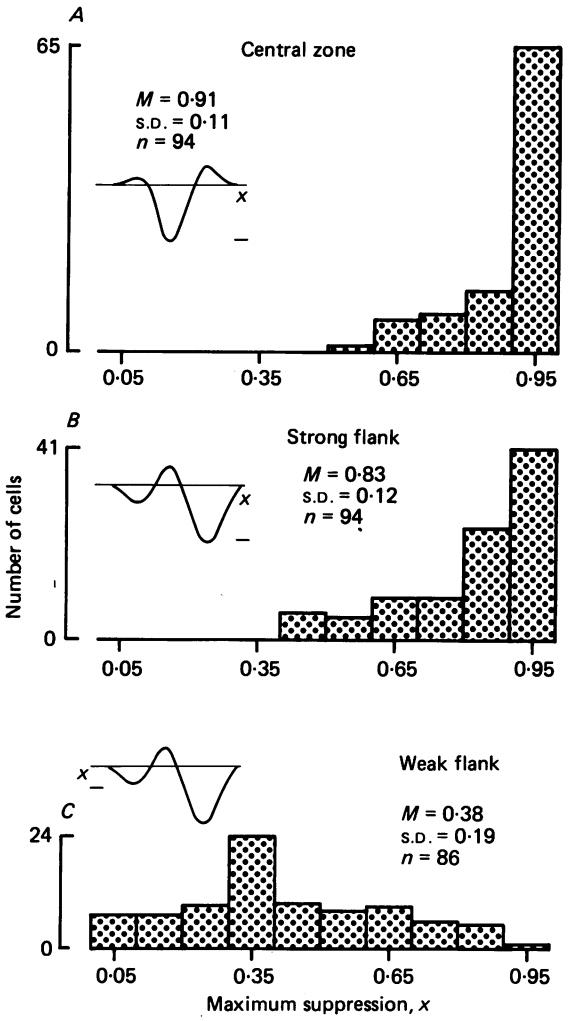

Fig. 3. Frequency distributions for the maximum suppression. The suppression was defined by 1 − c.s./a.s., where c.s. is the response to combined slit presentation and a.s. the response to the activation slit alone. The parameter which was measured is indicated by x on the schematic activation profile inserted beside each of the histograms. *A*, the suppression in the central zone when the test and activation slits were flashed in counterphase. *B*, the suppression in the strong proximal flank zone when the slits were flashed in phase. *C*, the suppression in the weak proximal flank zone when the slits were flashed in phase. Abbreviations in this and subsequent Figures: *M*, arithmetic mean; S.D., standard deviation; *n*, number of values.

Four cells had only one flank zone adjacent to the central zone in the activation profile made by flashing the slits in phase. Three of these were S3 cells. Fig. 2 shows results from one of them. This cell differed from the others by having enhancement on the weak flank zone (Fig. 2*C*). The fourth cell was an S2 cell which had no enhancement on the flanks when the slits were flashed in counterphase. This cell was therefore the only one which had not more than two subzones in either the discharge field plot or the activation profiles. The four cells with only one flank suppression

zone were extreme cases on a continuum rather than representing a separate category, as shown by Fig. 3*C* where the frequency distribution of the maximum suppression on the weak flank is presented for the whole sample of cells.

The flank zones adjacent to the central zone were termed *proximal flank zones*. Distal to these some cells had an additional subregion. In the profiles determined by flashing the slits in phase, enhancement occurred in these zones, and in the profiles made by flashing the slits in counterphase, suppression occurred. For twenty-eight cells the part of the receptive field which was plotted was too narrow to decide whether such zones existed. Of the residual sixty-six cells thirty-five (53%) had a distal zone only adjacent to the strong proximal flank zone. In seven cells (10·6%) a distal zone occurred adjacent to both proximal flank zones (Fig. 4). No cells had a distal zone only on the weak flank. In twenty-four cells (36·4%) no distal effects occurred.

The enhancement and suppression effects in the distal flank zones were usually weak, and there seemed to be a continuum of different degrees of the effects in the sample of cells. The distal flank zones were found among all the subclasses of S1–S5.

Relative location of discharge and enhancement or suppression zones

The receptive field subregions defined by on- and off-zones in the discharge field plot were also seen in the same parts of the receptive field as enhancement and suppression zones defined by the activation profiles (Figs. 1, 4 and 5).

The position in a subregion where the single slit elicited maximum discharge was the same in most cells as the position where maximum enhancement and maximum suppression occurred in the double-slit experiments. The distance between the position where maximum discharge occurred and where maximum enhancement or suppression occurred was measured, and expressed relative to the width of the most responsive zone in the discharge field plot (the dominant discharge zone). In the central zone the relative distance between the position where the maximum response occurred in the single-slit experiment and the position where maximum enhancement occurred in the dual-slit experiment, varied between 0 and 0·5 from cell to cell. The average relative distance was 0·12 (S.D. = 0·15). The corresponding average distance between the position with maximum single-slit response and the maximum suppression when the test and activation slits were flashed in counterphase was 0·15 (S.D. = 0·17). In the strong flank zone the average distance between the discharge maximum for a single slit to the maximum suppression when the slits were flashed in phase was 0·17 (S.D. = 0·18) for the S2–S5 cells. The average distance between the response maximum to a single slit and the response maximum when the dual slits were flashed in counterphase was 0·19 (S.D. = 0·19). The intervals between the test slit positions used in the receptive field plots were 0·2–0·3 deg, and the average distances between the maximum and minimum points in a subregion were within the resolution of the measurements. On the weak flank the corresponding distances were calculated for the S3–S5 cells. These values were not significantly different from the values for the strong flank. Hence, in the central zone and in the proximal flank zones the maximum discharge and the maximum suppression or enhancement effects occurred in the same receptive field position.

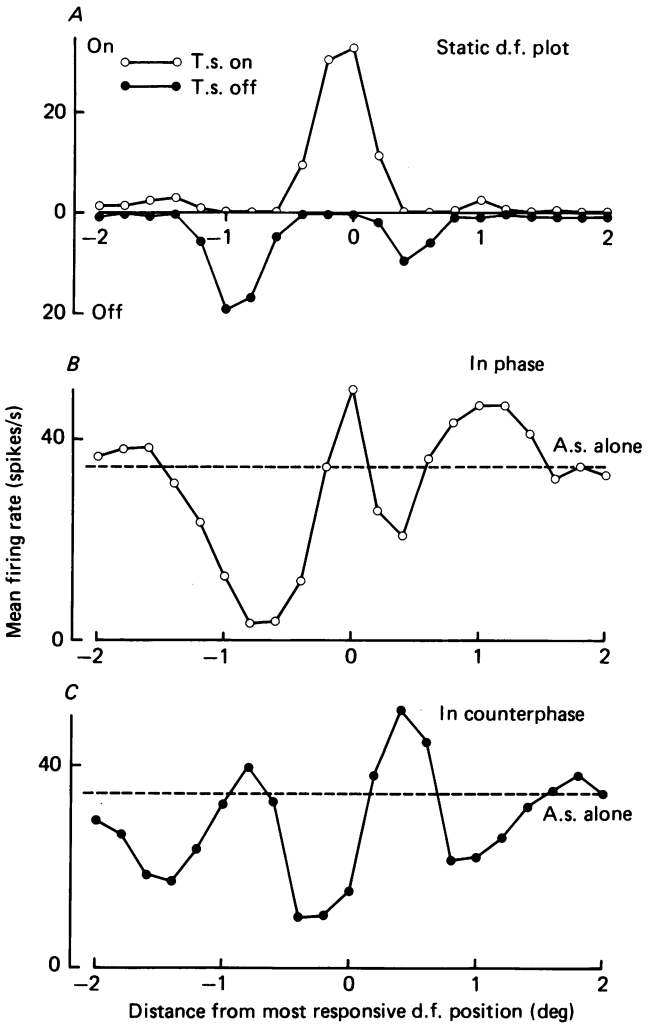

Fig. 4. Response profiles across the receptive field for an on-dominant simple cell. *A*, static discharge field plot made with a single slit which was flashed on and off in different positions across the receptive field. ○, discharge to slit on; ●, discharge to slit off. *B*, static activation profile which shows the response to the test and the activation slit flashed on in phase. The on-response to the activation slit alone is indicated by the dashed horizontal line. *C*, static activation profile showing the response of the cell when the two slits were flashed in counterphase (a.s. on, t.s. off). The on- and the off-periods were 500 ms, and sixteen measurements were obtained for each test slit position. The slit dimensions were 0·2 × 3·4 deg.

The close correspondence between location of maximum discharge and maximum enhancement or suppression effects did not mean that each subzone could be identified by both types of effects. Many receptive field zones were only manifest in the activation profiles since the single slit elicited no discharge. This was the case for the flank zones of the S1 cells, and for the weak proximal and the distal flank zones of the S2 cells. Hence, when discharge to a single slit occurred in a subregion, the

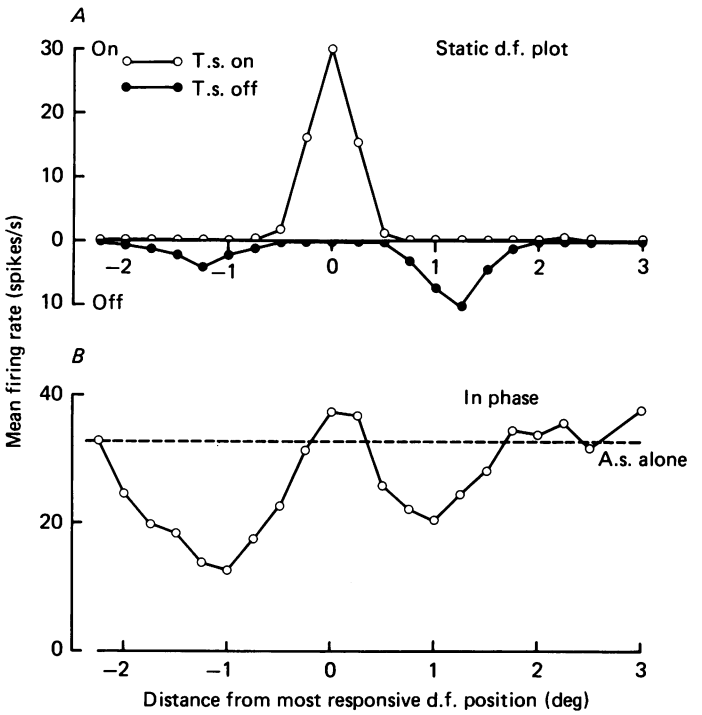

Fig. 5. Response profiles across the receptive field for an on-dominant simple cell. *A*, static discharge field plot made with a single slit which was flashed on and off in various broadside positions across the receptive field. ○, on-discharges; ●, off-discharges. *B*, static activation profile made with test and activation slit flashing on in phase. The on-response to the activation slit alone is indicated by the dashed horizontal line. The on- and off-periods were 500 ms, and sixteen measurements were obtained for each test slit position. Slit dimensions were 0·23 × 4·1 deg.

maximum discharge was in the same position as the maximum suppression and maximum enhancement in the zone.

Discharge and suppression

For eighty-one cells (86·2 %) the strongest flank suppression occurred in that of the two proximal flank zones which had the strongest discharge to a single slit. Nevertheless, there was no correlation between the degree of discharge and the degree of suppression in the proximal flank zones. The degree of discharge to a single slit therefore gave no information about the degree of suppression. The fact that all S1 cells had proximal flank zones showed that strong suppression could occur where a single slit elicited no discharge (Fig. 1). The opposite relationship was seen in three S3 cells. A single slit elicited discharge on the weak flank although no suppression occurred there (Fig. 2*A* and *B*). Seven cells (7·4 %) had strongest suppression in the flank zone which had the weakest response to the single slit (Fig. 5).

A correlation coefficient between the maximum discharge to a single slit and the maximum suppression by the dual-slit condition was calculated for each of the

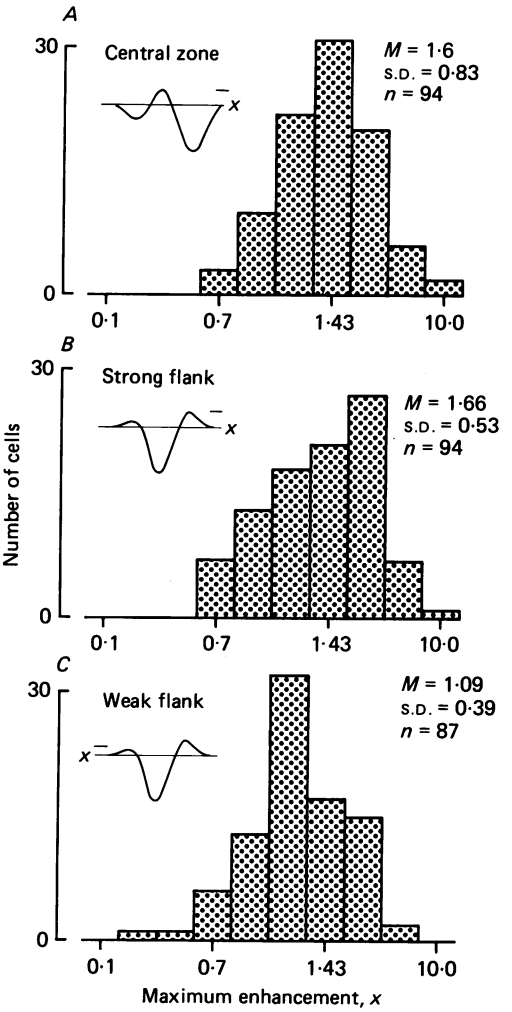

Fig. 6. Frequency distribution for the maximum enhancement in the central zone when the test and activation slits were flashed in phase (*A*), in the strong proximal flank zone when the two slits were flashed in counterphase (*B*), and in the weak proximal flank zone when the slits were flashed in counterphase (*C*). The measured parameter is indicated by x in the inset schematic activation profile. The abscissa was defined by c.s./a.s. where c.s. is the response to combined slit presentation, and a.s. the response to the activation slit alone. Values above 1 show enhancement.

proximal flank zones. The single-slit discharge was expressed as percentage of the maximum response in the dominant discharge zone. The correlation coefficient for the strong flank zone was 0·02 and for the weak flank zone 0·18, showing that there was hardly any covariance between the relative on- or off-response and the suppression in the proximal flank zones.

The fact that the strongest flank suppression usually occurred in the proximal flank zone with the strongest single-slit response could indicate that there is a correlation between the degree of asymmetry of the discharge and degree of asymmetry of

suppression in the proximal flank zones. Therefore the correlation coefficient between the ratio of the maximum discharge in the weak and strong flank zones in response to a single slit, and the ratio between the maximum suppression in the proximal flank zones was calculated for all S3–S5 cells. The coefficient was 0·21, showing that there was also little covariance between these parameters.

Degree of enhancement and suppression

In the central zone the ratio between the maximum response to both slits flashed in phase and the response to the activation slit alone, had a mean of 1·6 (S.D. = 0·83). The average maximum response to both slits was therefore 60 % above the response to the activation slit alone. The frequency distribution of these ratios was unimodal (Fig. 6*A*). In the strong flank zone the corresponding ratios calculated for the test-slit position where the response maximum occurred when the two slits were flashed in counterphase (Fig. 6*B*) had a mean of 1·66 (S.D. = 0·53). The corresponding mean on the weak flank (Fig. 6*C*) was 1·09 (S.D. = 0·39). The average maximum enhancement on the strong proximal flank zone was therefore the same as in the central zone, whereas the average maximum enhancement on the weak proximal flank zone was significantly lower ($P < 0·001$).

The degree of suppression was defined by the formula $1 - \text{c.s./a.s.}$ where c.s. is the response to combined slit presentation and a.s. the response to the activation slit alone. The variation of maximum suppression in the central zone when the two slits were flashed in counterphase is shown in Fig. 3*A*. The average maximum suppression was 91 %. On the strong flank the average maximum suppression (Fig. 3*B*) was 83 % and thereby slightly less than in the central zone ($P < 0·01$). Hence, also with respect to average maximum suppression only small differences were seen between the central zone and the strong proximal flank zone. The frequency distributions (Fig. 3*A* and *B*) showed, however, that 90–100 % suppression occurred more frequently in the central zone than in the strong proximal flank zone.

The maximum suppression in the weak flank zone had a mean of 0·38 (S.D. = 0·19). The ratio between the maximum suppression on the weak and the strong proximal flank zone had a mean of 0·27 (S.D. = 0·26). Hence, the average maximum suppression on the strong flank was 3·7 times stronger than on the weak flank. The maximum response on the two flanks when the two slits were flashed in counterphase showed less asymmetry. The average ratio between the response in the weak and in the strong proximal flank zone in this condition was 0·67 (S.D. = 0·22), which means that the maximum response in the strong flank zone was on average 1·5 times stronger than the maximum in the weak flank zone.

Width of the subzones

The width of a subzone was measured in three different ways: first, by the extension over which the single slit elicited on- or off-response in the discharge field plot; secondly, as the extension of enhancement effects in the zone measured by one of the activation profiles; and thirdly, as the extension of suppression effects measured by the other activation profile. All three measures for the width increased with receptive

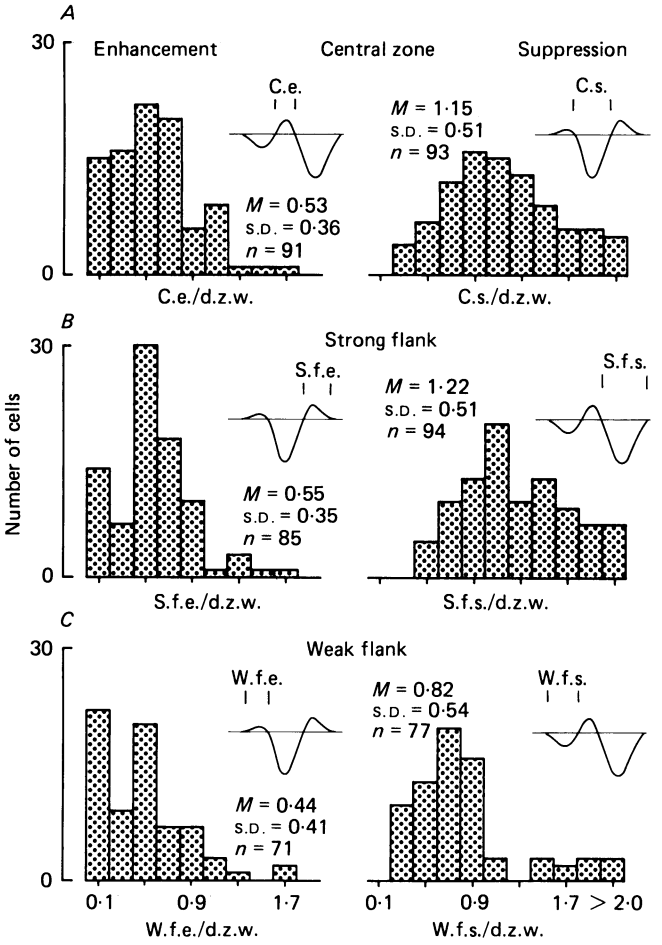

Fig. 7. Frequency distributions showing the width of the subregions in the activation profiles determined by the double-slit experiments. All widths are expressed relative to the width of the dominant discharge zone (d.z.w.) for the cell, i.e. the zone in the discharge field plot where the strongest response to the single slit was obtained. The measured parameters are indicated by x on the inset schematic activation profiles. *A*, the width of the central zone defined by the enhancement effects occurring when the slits were flashed in phase (c.e., left histogram), and by the suppression effects when the slits were flashed in counterphase (c.s., right histogram). *B*, the width of the strong proximal flank zone defined by the enhancement effects when the slits were flashed in counterphase (s.f.e., left histogram) and by the suppression effects when they were flashed in phase (s.f.s., right histogram). *C*, the width of the weak proximal flank zone defined by the enhancement effects (w.f.e., left histogram) and by the suppression effects (w.f.s., right histogram).

field eccentricity. The sample of cells was too small to give representative measures at the various eccentricities. The widths were therefore expressed relative to the width of the dominant discharge zone for the cell.

The variation of the width parameters for the central zone is shown in Fig. 7*A*. The enhancement region was on average 47% narrower than the dominant dis-

charge zone, and the suppression region 15% wider. The width values for the strong proximal flank zones were almost equal to the values for the central zone, as shown by Fig. 7*B*, but the weak flank (Fig. 7*C*) was narrower for most cells. The average width of the dominant discharge zone for these cells was 1·45 deg (S.D. = 0·63 deg).

The width of the whole receptive field was defined by the range across the activation profiles where the test slit would influence the response to the activation slit. Also this measure was expressed relative to the width of the dominant discharge zone. The width varied between 1·8 and 6·9 with a mean of 3·05 (S.D. = 1·04, $n = 66$). The mean width of the whole discharge field for the same cells was 1·93 deg (S.D. = 0·60 deg). Thus, the average width of the whole receptive field was 4·42 deg. The receptive field width measured by the activation profiles was therefore on average 2·3 times wider than the discharge field measured by a single slit. This discrepancy was mainly due to the many subregions which were only revealed by the activation profiles.

Distance between extreme points of the activation profiles

The distance from the most responsive position in the central zone to the most responsive position in the proximal flank zones was also measured in three different ways: first, as the distance between the position with maximum discharge in the central zone and the position with maximum discharge in the proximal flank zones given by the discharge field plots; secondly, as the distance from the position of the response maximum in the central zone to the position of the response minimum in the respective flank zone determined by the in-phase activation profile; thirdly, as the distance from the position of the response minimum in the central zone to the response maximum in the respective flank zone determined by the in-counterphase activation profile. No statistically significant differences were found between the three different measurements.

Fig. 8 shows the frequency distribution of the distance from the response maximum in the central zone to the response minimum in the strong flank zone (Fig. 8*A*), and to the response minimum in the weak flank zone (Fig. 8*B*). The distances were expressed relative to the width of the dominant discharge zone of the respective cell. For the majority of cells no clear differences were found between the distances from the response maximum in the central zone to the response minimum of the proximal flank zones. When differences did occur the distance to the response minimum on the weak flank zone was usually smallest.

The most responsive position in the distal flank zones was difficult to determine precisely in some of the profiles due to the weak response. Nevertheless, in the majority (twenty-seven of thirty-five cells) of the cells where this could be done, the distance from the most responsive position in the strong proximal flank zone to the most responsive position in the adjacent distal flank zone, was about the same as the distance between the extreme values of the central and the proximal flank zone. Hence, for these cells the distances between the successive extreme points across the activation profile were about constant. For five cells the distance from the extreme point in the proximal to the extreme point in the distal flank zones was about twice the distance between the extreme points of the central zone and the proximal flank zones. The sample of cells was too small to decide whether such doubling of the

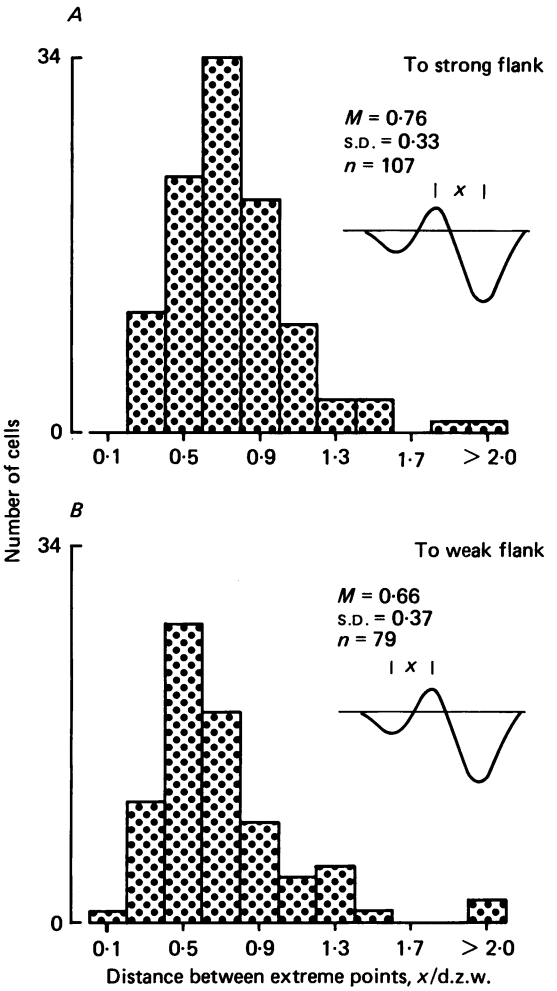

Fig. 8. Frequency distributions for the distance between extreme points in the activation profiles determined by the double-slit experiments when the two slits were flashed in phase. The distances were expressed relative to the width of the dominant discharge zone (d.z.w.) for the cell, i.e. the zone in the discharge field plot where the strongest response to the single slit occurred. *A*, distance between the position with maximum response in the central zone and the position with minimum response in the strong proximal flank zone. *B*, distance between the extreme point in the central zone and in the weak proximal flank zone.

distance to the distal flank zones was characteristic for a group of simple cells, or just special cases on a continuum of different distances.

For almost all cells the distance from the response maximum in the central zone to the response minimum in the proximal flank zones was smaller than the width of the dominant discharge zone, as shown by Fig. 8. This was mainly because the response minima in the flank zones occurred proximal to the mid-point of the respective proximal flank zone.

DISCUSSION

The activation profiles showed less variation in number of receptive field subregions than the discharge field plots. Whereas the number of discharge zones varies between one and five (Heggelund, 1986) all the cells except one had at least three subregions, and only 10% had as many as five subregions when both discharge field plot and activation profiles were considered. Hence, almost all the cells had a receptive field with a central zone and two adjacent flank zones. It is therefore unlikely that the differences between S1 and S2 cells reflect basic differences of intracortical connectivity as has been suggested (Orban, 1984).

The effects in the distal flank zones were weak, but nevertheless such effects occurred in more than 50% of the cells. The cells with distal flank zones could represent units with genuinely different receptive field organization. Alternatively, the receptive field organization of all the cells could be the same, but the distal zones were too weak in many cells to be detected by the measurement procedure used. The latter alternative is most likely since the distal effects varied from cell to cell from clear effects to just noticeable effects. Furthermore, a distal flank zone was frequently seen on the strong flank but rarely on the weak flank. Accordingly, the general receptive field of simple cells seemed to consist of a series of adjacent, oppositely responding subzones. The central zone was most responsive and the responsivity usually decreased the further a subregion was from the central zone. The responsivity of the flanks was asymmetric.

The distance between successive extreme points across the activation profile was about the same for most cells. This, combined with the general wave-form pattern of the activation profiles, can explain the selectivity for spatial frequency of periodic stimulus pattern (Campbell, Cooper & Enroth-Cugell, 1969; Maffei & Fiorentini, 1973; Ikeda & Wright, 1975; Movshon, Thompson & Tolhurst, 1978; Andrews & Pollen, 1979; Albrecht & De Valois, 1981; Kulikowski & Bishop, 1981). The distance from one extreme point to the next across the activation profile should be equal to $\frac{1}{2}$ cycle of the optimum spatial frequency of the cell to periodic gratings. Movshon *et al.* (1978) found that optimum spatial frequency for sinusoidal gratings varied between 0·3 and 2·2 with a mean of 0·86 cycles/deg (S.D. = 0·48) for simple cells in area 17 within 0–5 deg eccentricities. Thompson & Tolhurst (1979) found a range of 0·25–2·5 cycles/deg at eccentricities within 3 deg. Using the values in Fig. 8 for the distance between the extreme points to predict the optimum spatial frequencies, and a value for average dominant discharge zone of 1·12 deg at 3 deg eccentricity (Heggelund, 1986), the range of optimum spatial frequencies would be 0·26–2·35 cycles/deg with a mean of 0·63.

The location of a subregion determined by the discharge field plot corresponded well with the location determined by the activation profiles. Not all subregions in the activation profiles had a counterpart in the discharge field map, reflecting that the activation method was more sensitive for detecting subregions of the receptive field. In a given subregion the width over which enhancement effects occurred was considerably narrower than the corresponding discharge zone, and the suppression region was slightly wider. A major difference between the single- and double-slit tests was the degree of cell activation, which was raised in the double-slit experiments.

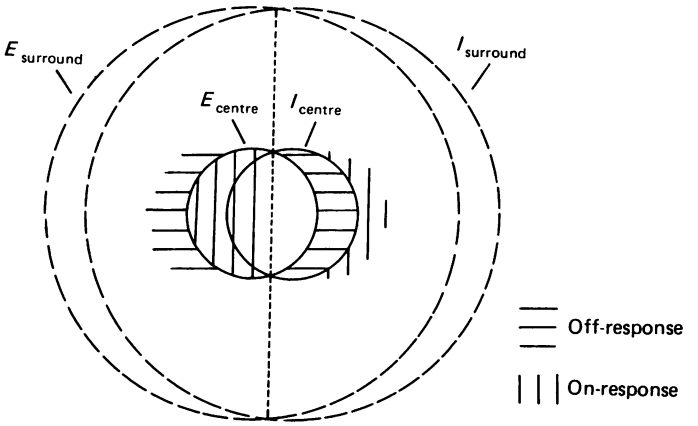

Fig. 9. Schematic illustration of the receptive field configuration of an on-dominant simple cell according to a model (Heggelund, 1981) presuming that simple cells have direct excitatory (*E*) and indirect inhibitory (*I*) input from l.g.n. fibres with concentric centre–surround receptive fields. Both l.g.n. cells are assumed to be on-centre neurones. The dashed vertical line indicates the theoretical locus where no response can be elicited from the simple cell presuming equal weight of excitatory and inhibitory input. Strong on-response would occur from part of the receptive field centre of the excitatory input field. Relative strong off-response would occur from part of the receptive field centre of the inhibitory input field due to suppression of the inhibitory input by light-off which would disinhibit off-discharge from the surround of the excitatory input fibre. The other subregions are presumed to occur from different balances of the receptive field surround of the excitatory and the inhibitory input fibres.

The results indicate that the degree of suppression increased with cell activation (Sillito, 1979; Heggelund, Krekling & Skottun, 1983) causing the enhancement zone to shrink relative to the discharge zone, and the suppression zone to widen. Such variations in the width of subregions were found by Heggelund *et al.* (1983) who studied spatial summation in simple cell receptive fields. They suggested that the extension of a subregion is determined by overlapping excitatory and inhibitory fields, and that both the excitatory and the inhibitory input is a compressed function of the degree of activation of the respective input cell. The width of the subregion would then vary according to an activation-dependent balance between the excitatory and inhibitory input to the cortical cell.

Bishop, Coombs & Henry (1973) determined the extension of enhancement and suppression zones for eighteen simple cells with receptive fields within 3 deg from the visual axes. They used asynchronously moving activation and test slits. By movement of the test slit in the null direction suppression occurred throughout the receptive field which on average was 4·2 deg across. By movement of the slit in the preferred direction the receptive field was organized into a central discharge zone and adjacent suppression flanks. Some cells showed weak enhancement distal to the suppression flanks. The average width of the whole receptive field was 3·9 deg, the central zone 0·6 deg, and the suppression flanks 1·3–2·0 deg. The narrow width they found on the central zone compared with the suppression flanks could be due to a shrinkage of the central zone caused by the increased activation, as discussed above. The comparable

width values from the static experiments can be calculated by correcting for the width of the dominant discharge zone at 3 deg eccentricity (1·12 deg: Heggelund, 1986). This gives an average width of the whole receptive field of 3·5 deg, a width of the central enhancement zone of 0·6 deg, and a width of the strong suppression flank zone of 1·4 deg. Thus, the configuration and dimensions of the simple cell receptive fields plotted with static stimuli corresponded well to the results obtained with moving stimuli. Therefore moving stimuli do not seem to reveal any spatial receptive field properties additional to those found with static stimuli. However, the static experiments showed that both the central zone and the flank zones respond with enhancement or suppression depending on the light cycle, and that the central zone and the strong proximal flank zones were about equally wide. Furthermore, the results with static stimuli showed the spatial organization of the receptive field independent of movement direction.

Despite the close correspondence between location of discharge and suppression zones, there was no correlation between the degree of discharge and the degree of suppression in the proximal flank zones. This indicates that there is a common restricting condition which determines the location of suppression and the location of discharge, but that the factors determining the degree of suppression and degree of discharge are independent. The width of the central zone and the width of the strong proximal flank zone were remarkably similar, but wider than the weak proximal flank zone. Also, with respect to the maximum enhancement and maximum suppression, the central zone and the strong proximal flank zone were similar. These results are consistent with the model presuming that the simple cell receptive field is produced by an excitatory field overlapping an inhibitory one, with the centre of the two fields being slightly offset and both fields having input only from on- or only from off-centre cells of the lateral geniculate nucleus (l.g.n.) (Heggelund, 1981). This is illustrated by Fig. 9 for an on-dominant simple cell. The extension of the central zone would be produced primarily by the receptive field centre of the excitatory l.g.n. cell. The extension of the strong proximal flank zone would be produced primarily by the receptive field centre of the inhibitory l.g.n. cell. Accordingly, the central zone and the strong proximal flank zone would become almost equally wide. The weak proximal flank zone would be produced by the surround of the excitatory l.g.n. cell. The off-response in the proximal flank zones would be primarily due to surround response of the excitatory l.g.n. cell. The off-response on the strong flank zone would be amplified within the area covered by the receptive field centre of the inhibitory field because there would be no inhibition by light-off there. In fact it would be disinhibition, so even spontaneous activity from the excitatory input fibres could come through. The location of the receptive field centre of the inhibitory input fibres would accordingly bound both the suppression zone and the off-response zone and thereby account for the good correspondence between the location and width of the two regions. The degree of suppression would primarily depend on the weight of inhibition relative to the excitation. The degree of off-response would depend primarily on the centre–surround balance of the excitatory on-centre neurones. This could explain the lack of covariance between the degree of suppression and degree of discharge.

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