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QUANTITATIVE STUDIES OF THE DISCHARGE FIELDS OF SINGLE CELLS IN CAT STRIATE CORTEX

BY P. HEGGELUND*

From the Neurobiological Laboratory, University of Trondheim, N-7055 Dragvoll, Norway

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SUMMARY

1. The configuration and width of on- and off-response zones in the discharge field of single cells in cat striate cortex was analysed by quantitative methods. The responses across on- and off-zones were plotted for 321 cells with a stationary optimum oriented light slit.

2. The cells fell into two completely distinct subgroups with respect to the degree of overlap between adjacent on- and off-zones. The simple cells had a mean overlap of 16·8 %, the complex cells 94·5 %. For simple cells the ratio between the maximum off- and maximum on-response in the discharge field was bimodal, showing that two distinct subgroups termed on- and off-dominant cells could be distinguished. For the complex cells the corresponding frequency distribution was unimodal.

3. The maximum response on the two regions adjacent to the most responsive discharge zone (the dominant zone) differed markedly for most simple cells, and only a very few cells had discharge fields approximating an ideal even symmetric field. The frequency distribution of the ratio between the maximum response in the two regions was unimodal showing that odd and even symmetric fields did not form distinct subgroups of simple cells.

4. The number of different discharge zones in simple cells varied from one to five. The zones were arranged as alternating on- and off-zones across the discharge field. The maximum response in the subzones decreased with increasing sequential distance from the dominant zone, so the response pattern across each side of the discharge field resembled a damped wave-form pattern. All the complex cells had one on- and off-zone which overlapped.

5. The mean width of the subregions in the simple cell discharge field and the mean distance between the response maxima in the subzones increased in the same proportion with increasing eccentricity. The paracentral fields were therefore like magnified central fields. The average width of the whole discharge field was not significantly different for the simple and the complex cells at the various eccentricities.

* Present address: Institute of Neurophysiology, University of Oslo, Karl Johans Gt. 47, Oslo 1, Norway.

INTRODUCTION

The cells in cat striate cortex vary widely with respect to the configuration of on- and off-response zones in the discharge field determined by a stationary flashing light stimulus. Hubel & Wiesel (1962) described several such configurations for both simple and complex cells. Some simple cells had bipartite fields consisting of adjacent on- and off-zones with almost equally strong response in the two zones. Other simple cells had tripartite discharge fields consisting of a centrally located on- or off-zone flanked by weaker response zones of the opposite type on each side, and with almost equally strong response on each flank. Such bipartite and tripartite fields have later been termed odd and even symmetric, respectively (Robson, 1975). Movshon, Thompson & Tolhurst (1978) classified 62% of the simple cells as odd symmetric and 38% as even symmetric. They mentioned, however, that this categorization to some extent was artificial since receptive fields with intermediate properties occurred. Palmer & Davis (1981) studied subtypes of simple and complex cell receptive fields by analysis of peristimulus–time response planes (Stevens & Gerstein, 1976). They subclassified simple cells into four distinct subgroups termed S1–S4 depending on the number of separate on- and off-response zones. Two subgroups of complex cells were distinguished. C1 cells had only a single on- or off-response zone, and C2 cells had spatially overlapping on- and off-zones.

In the present study the configuration and extension of subregions in the receptive field of striate cortex cells were analysed quantitatively with stationary flashing stimuli. In this paper data are presented on subregions of the discharge field determined with a flashing light slit. In the following paper (Heggelund, 1986) data on enhancement and suppression zones in the receptive field determined by a dual slit technique (Heggelund, 1981*a*) are presented. The results from the discharge field analyses showed that simple cells could be subdivided into two distinct subclasses termed on- and off-dominant cells depending on the light change which most effectively activated the cell. All the simple cells had asymmetric receptive fields, and only a very few cells had fields approximating the ideal even symmetric type. Only complex fields with overlapping on- and off-zones were found.

METHODS

The general methods were described in detail by Heggelund (1981*a*). Adult cats (3–5 kg) were prepared surgically for single-unit recording under pentobarbitone anaesthesia, and light anaesthesia was maintained throughout the recording session by intermittent pentobarbitone doses when necessary. E.e.g., e.c.g., end-tidal CO_2, and rectal temperature were monitored continuously during the experiments. Eye movements were reduced to very low levels by continuous infusion of 20 mg gallamine triethiodide (Flaxedil) and 1 mg toxiferindichloride (Alloferin) per hour, combined with bilateral cervical sympathectomy. Contact lenses focused the eyes on a tangent screen 1 m from the cats' eyes. Artificial pupils with 5 mm diameter were used.

Extracellular single-unit recordings were made with glass-insulated tungsten electrodes (Levick, 1972) in long electrode penetrations down along the medial bank of the post-lateral gyrus at Horsley-Clark coordinates posterior 2–5 mm, lateral 0·5–1·5 mm. Optimum stimulus orientation, ocular dominance, direction asymmetry, and minimum response field (Barlow, Blakemore & Pettigrew, 1967) were determined with a hand-held projector. The rest of the analysis was made with a computer-controlled light projector.

First, the optimum stimulus orientation of the cell was determined from an orientation tuning curve made with a computer-controlled moving light slit. Secondly, a plot of the discharge field was made with an optimum oriented, stationary light slit which was flashed on and off in a series of broadside positions across the discharge field (static discharge field plot). Slit length, width and luminance 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 luminance which was about 5 cd/m^2. In each slit position a peristimulus–time histogram (p.s.t.h.) was determined for the response of the cell. The time window of the on- and off-period was equal but varied from cell to cell between 0·5 and 1·0 s. The slit was only flashed once in each position, and when all positions had been tested the sequence was repeated. The number of times this sequence was repeated varied from cell to cell between 10 and 30. The on- and off-response was defined by the mean firing rate during the on- and the off-period, respectively.

RESULTS

The on- and off-response to an optimum oriented light slit was plotted across the discharge field for 322 striate cortex cells. All the cells had their discharge field centred within 13 deg from the visual axes.

Simple and complex cell classification

Degree of overlap between on- and off-zones

One of the criteria introduced by Hubel & Wiesel (1962) to distinguish simple from complex cells was that simple cells have discharge fields which are subdivided into distinct on- and off-zones. Some investigators have later used this criterion exclusively to distinguish the two cell classes (Albus, 1975; Singer, Tretter & Cynader, 1975; Heggelund, 1981*a*; Toyama, Kimura & Tanaka, 1981) and defined cells with spatially distinct on- and off-zones as simple, and cells with spatially overlapping on- and off-zones as complex. However, in some cells with separate on- and off-zones there is a certain overlap between the two types of zones, and in some of the cells with mixed on- and off-discharge field the overlap of the on- and off-zones is not complete. The question therefore arises whether there are really two distinct classes of cells with respect to the degree of overlap between on- and off-zones, or a continuum of cells with different degrees of overlap. To analyse this the degree of overlap of the on- and off-discharge zones was measured for all the cells except for six which had only a pure on- or a pure off-zone in the receptive field. For the cells which had more than two discharge regions the degree of overlap was measured for the two most responsive, adjacent zones. The measure of the degree of overlap was expressed relative to the width of the most responsive discharge zone.

The cells fell into two completely distinct groups, as shown by Fig. 1. Cells in the one group had no or only a moderate degree of overlap. For 61 % of these cells the overlap was 10 % or less. The average degree of overlap was 16·8 % (S.D. = 15·8 %). The cells in the other group had complete or almost complete overlap of the on- and off-discharge zones. For 60 % of these cells the overlap was complete, and for 75 % of the cells the degree of overlap was 90 % or larger. The average degree of overlap for this group was 94·5 % (S.D. = 8·9 %). The cells in the first group with no or only moderate overlap between the on- and the off-zones were defined as simple cells. The six cells which had only a single discharge zone (on or off) were also included in the simple cell class because they had a strong suppression zone adjacent to the discharge

zone (Palmer & Davis, 1981) as shown in the following paper (Heggelund, 1986). The cells in the second group with complete or almost complete overlap of the on- and off-zone were defined as complex cells. Of all the cells, 69 % (n = 222) were classified as simple and 31 % (n = 100) as complex.

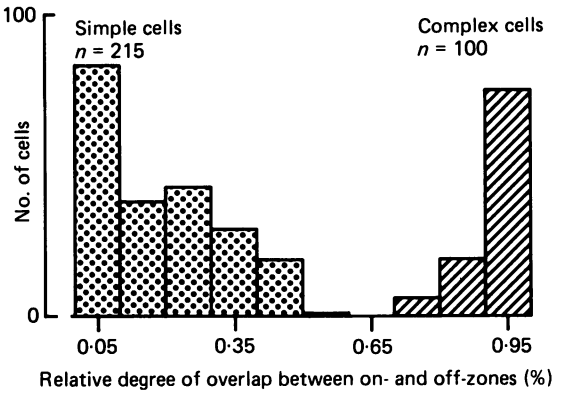

Fig. 1. Frequency histogram which shows the degree of overlap between on- and off-zones in the discharge field of the cells. For cells with more than one on- and one off-zone the overlap was measured for the two most responsive adjacent subzones. The overlap was expressed relative to the width of the most responsive discharge zone (the dominant zone). The cells fell into two distinct subclasses. The cells with moderate or no overlap (dotted columns) were defined as simple cells and those with complete or almost complete overlap (hatched columns) were defined as complex cells.

Simple cells

The relative strength of the on- and off-responses, as well as the spatial arrangement of on- and off-zones, varied widely among simple cells, as originally described by Hubel & Wiesel (1962). With respect to both these characteristics it was possible to distinguish different subclasses of simple cells.

On- and off-dominant simple cells

For most simple cells the maximum response to a light slit in the most responsive on-zone was clearly different from the maximum off-response in the most responsive off-zone. The simple cells could therefore be subdivided into on- and off-dominant cells depending on the type of response which was strongest (Heggelund, 1981*a*). To test whether these two categories refer to distinct subclasses of simple cells the ratio of the maximum on-response to the maximum off-response was calculated for each of the cells which had at least two discharge zones. The frequency distribution of this ratio is plotted in Fig. 2*A*. The histogram is clearly bimodal, showing that on- and off-dominant cells form two distinct subgroups of simple cells. One peak in the histogram occurred at 0·33 where the maximum off-response was three times the maximum on-response, and the other peak was at 3·0 where the maximum on-response was three times the maximum off-response.

The number of off-dominant cells was smaller than the number of on-dominant cells. The two halves of the frequency histogram became more symmetric when the

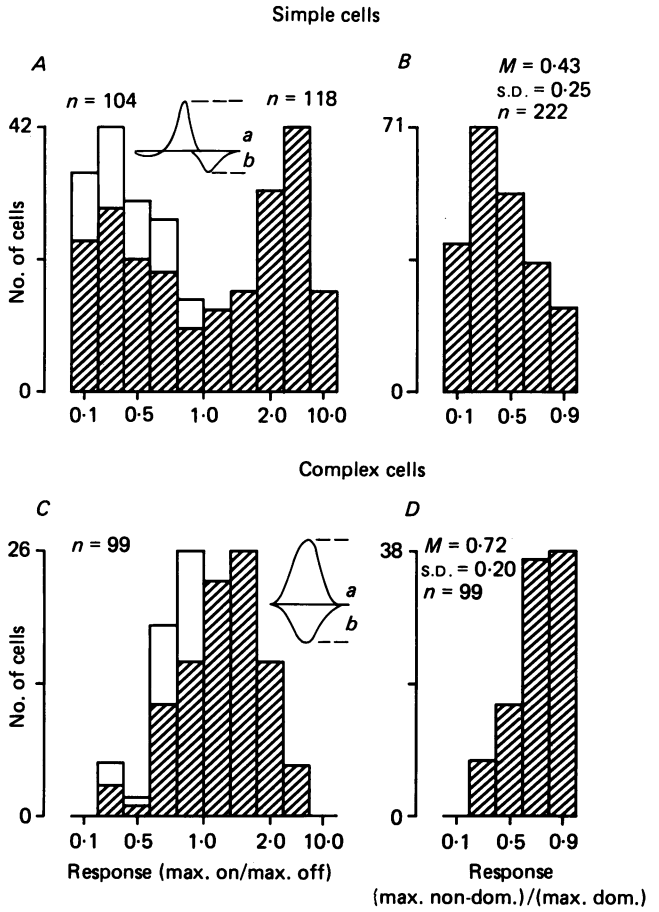

Fig. 2. Frequency histograms showing the balance between the maximum on- and off-response in simple (*A* and *B*) and complex cells (*C* and *D*). *A* and *C*: the maximum on-response divided by the maximum off-response (cf. inserted static discharge field plots where the curve above the abscissa indicates on-response and the curve below the abscissa the off-response) for simple (*A*) and complex cells (*C*). The number of cells where the maximum on-response was stronger than the maximum off-response (on-dominant cells, represented in the right half of the histograms) was larger ($n = 118$) than the number of cells with strongest off-response ($n = 104$). To compensate for this the left half of the histograms representing the off-dominant cells was scaled up to the same maximum ordinate value as the right half of the histogram. The resulting increases are shown by the unhatched part of the columns. *B* and *D*: the maximum non-dominant response divided by the maximum dominant response for simple (*B*) and complex cells (*D*). Abbreviations in this and subsequent Figures: *M*, arithmetic mean; S.D., standard deviation; *n*, number of values.

ordinates in the left half were normalized to the same maximum as the right half (increase by the unhatched parts of the columns). Even after this correction, however, the off-dominant cells were slightly more evenly distributed over the various class intervals than the on-dominant cells. This could be due to the fact that all the discharge fields were plotted with a light slit. A dark bar might have been a more comparable stimulus for the off-dominant cells.

For some cells the maximum on- and off-response were almost equally strong, and for eight cells the difference between the two maxima was less than 5%. For these cells the subclassification into on- or off-dominant simple cells was rather arbitrary. Nevertheless, the shape of the histogram in Fig. 2*A* indicates that these cells should

TABLE 1. Number of simple cells in the various subgroups S1–S5 defined by the number of discharge zones across the receptive field. Corresponding values from Palmer & Davis (1981) are shown in parentheses.

Subtype	*n*	Relative no.
S1	6	2·8% (21·3%)
S2	86	40·8% (41·1%)
S3	85	40·3% (32·2%)
S4	24	11·4% (2·4%)
S5	10	4·7% (0·0%)

be regarded as extreme cases within the subgroups of on- and off-dominant simple cells rather than as a separate subgroup.

For the on-dominant simple cells the off-response was termed the non-dominant response. For the off-dominant simple cells the on-response was termed the non-dominant response. The ratio between the maximum non-dominant and the maximum dominant response for each cell was calculated and the frequency histogram for the ratios is shown in Fig. 2*B*. The histogram had a mode at 0·3 and the mean ratio was 0·43 (S.D. = 0·25). Therefore the maximal non-dominant response was on the average 43% of the maximum dominant response.

Number of discharge zones

The four subgroups of simple cells described by Palmer & Davis (1981) distinguished by the number of discharge zones (S1–S4) were all observed also in the sample of cells of the present study (Fig. 3). In addition, also a fifth subgroup, S5, with five distinct discharge zones was found (see Fig. 3*H*). The proportion of on- and off-dominant cells was about the same in each subgroup except S1 where only one off-dominant cell was found. The number of cells in the five subgroups are shown in Table 1, together with the comparable numbers (in parentheses) from Palmer & Davis (1981). The most frequently occurring cells were S2 and S3 cells. The proportion of S4 and S5 cells were higher than the proportion of S1 cells. The proportion of S1 cells was very low, and of the six cells classified as S1 cells, four had a tendency toward non-dominant response on one side of the discharge field. Compared with the results of Palmer & Davis (1981) the distribution of cells in the present study was shifted toward more compound discharge fields with fewer S1 cells and more S3 and S4 cells, and in addition the S5 cells.

Although the subgroups S1–S5 were defined as distinct subclasses of simple cells, the sample of cells contained borderline cases between the various classes. Fig. 3*B* shows an off-dominant cell which had a weak on-zone on the right flank, illustrating an intermediate between an S1 and S2 type. Fig. 3*D* shows an intermediate between an S2 and S3 cell, and Fig. 3*F* shows an intermediate between an S3 and S4 cell.

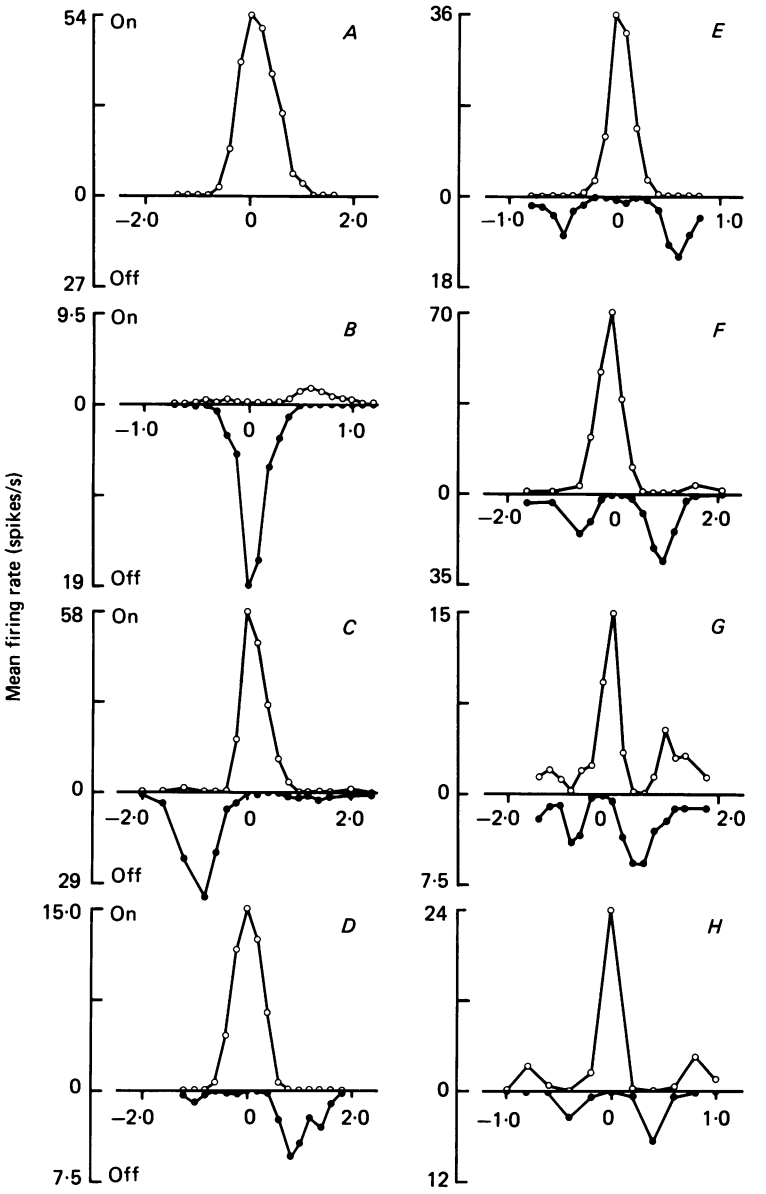

Fig. 3. Static discharge field (d.f.) plots for seven on-dominant simple cells (*A*, *C–H*) and one off-dominant cell (*B*) plotted with an optimum oriented light slit flashed ten times in each of a series of positions across the receptive field. The ordinates show the mean firing rate during the on- (○) and the off-periods (●). The on- and off-periods were 500 ms in all cases except *H* where they were 800 ms. The slit dimensions were in *A*: 0·23 × 2·88 deg; *B*: 0·17 × 4·00 deg; *C*: 0·17 × 3·26 deg; *D*: 0·23 × 1·78 deg; *E*; 0·23 × 1·78 deg; *F*: 0·17 × 3·32 deg; *G*: 0·17 × 2·12 deg; *H*: 0·11 × 1·72 deg.

Asymmetry in the discharge field profiles

To study whether cells with odd and even symmetric discharge fields can be regarded as two distinct subtypes of simple cells, the ratio between the maximum response on the two regions adjacent to the most responsive discharge zone (the dominant zone; see inset in Fig. 4) was calculated for each S2–S5 cell. The maximum response on the side with the weakest response was divided by the maximum on the side with the strongest response. The frequency histogram for the ratios is shown in Fig. 4.

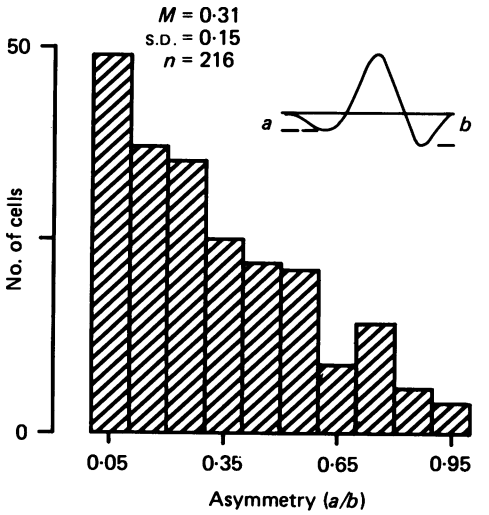

Fig. 4. Frequency histogram showing the degree of asymmetry in the maximum response in the regions adjacent to the dominant zone of the discharge field for all the S2–S5 cells. The abscissa shows the maximum response on the side with the weakest response divided by the maximum response on the side with the strongest response as indicated by the inserted static discharge field plot.

The histogram is unimodal, showing that odd and even symmetric fields were not distinct subtypes. In fact, all the S2–S5 cells had differing strong responses on the two sides of the dominant zone, and only a very few cells approximated the ideal even symmetric field. The mode of the frequency distribution was 0·05 and the mean ratio was 0·31 (S.D. = 0·15). Hence, the maximum response on the most responsive side of the dominant zone was about three times the maximum response on the least responsive side.

Spatial arrangements of on- and off-zones

The different configurations of on- and off-zones which occurred in the simple cells were only a small fraction of the possible combinations defined by the number of subregions. This was due to two restricting conditions. First, in all the discharge fields observed the adjacent subzones across the field were alternating on- and off-zones (Fig. 3). Secondly, the number of subzones on the two sides of the dominant zone differed at most by one. Fields with an odd number of subzones (S3 and S5) had the

same number of subzones on both sides of the dominant zone (Fig. 3*E* and *H*). Fields with an even number of subzones (S2 and S4) had one more subzone on one side than on the other.

The maximum response in the subzones was lower the further distal to the dominant zone a subzone was located, as illustrated by Fig. 3. Thus, distally from

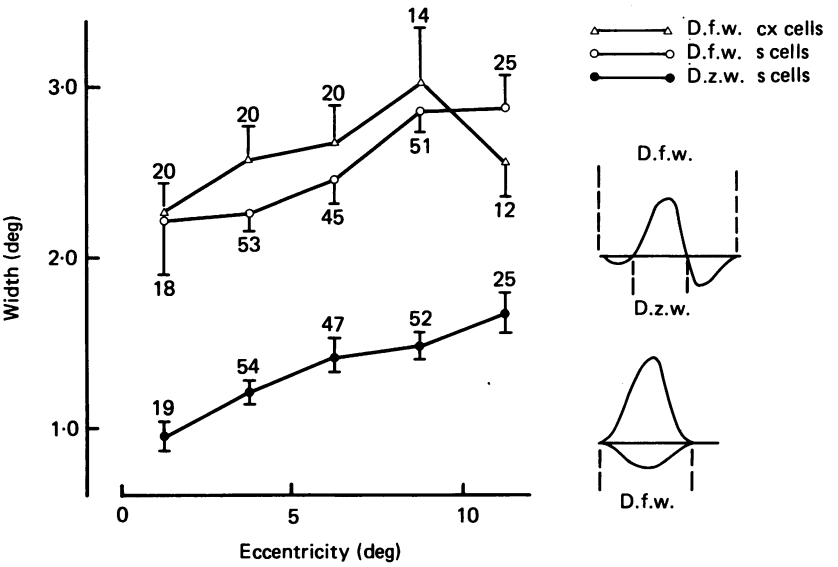

Fig. 5. Width of the discharge fields at different distances from area centralis. ●, width of the dominant zone (d.z.w.) of the simple cells (s); ○, width of the whole discharge field of the simple cells (d.f.w.); △ width of the whole discharge field of the complex cells (cx). The vertical bars show the standard error. The number of cells on which the mean values were based are indicated above or below each bar. The location of area centralis was determined according to the procedures of Bishop, Kozak & Vakkur (1962).

the dominant zone, the profile of on- and off-responses resembled a damped wave-form pattern.

The most distal subzone in the fields of the S4 cells was located distal to the most responsive non-dominant zone (Fig. 3*G*) in all except three cases. Thus, the fields looked as if a damped wave-form pattern was attenuated to different degrees on the two sides of the dominant zone, allowing more subzones to appear on the side with the weakest attenuation and causing the weaker distal subzones to disappear on the side with strongest attenuation.

Width of the discharge field

The width of the dominant zone was measured for each cell across the receptive field perpendicular to the optimum stimulus orientation. Spontaneous activity, if any, was subtracted before the width was measured. In Fig. 5 the mean width is plotted against eccentricity. The mean width increased from 0·95 deg (S.D. = 0·40) in the central 2·5 deg to 1·67 deg (S.D. = 0·63) at eccentricities of 10–12·5 deg. Within the

central 2·5 deg of the visual field the width of the dominant zone varied between 0·3 and 2·1 deg.

The width of the whole discharge field including all the subzones increased from a mean of 2·21 deg (S.D. = 1·31) in the central 2·5 deg to 2·88 deg (S.D. = 1·04) at eccentricities of 10–12·5 deg (Fig. 5). The whole discharge field was on average slightly less than twice the width of the dominant zone.

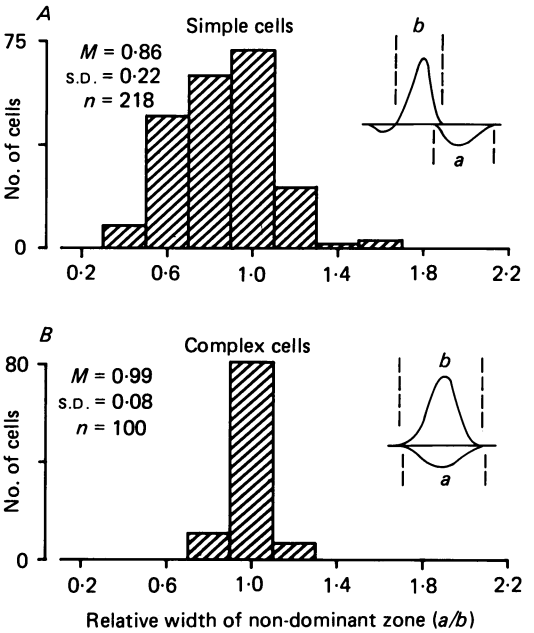

Fig. 6. *A*: width of the most responsive non-dominant zone (*a*) relative to the width of the dominant zone (*b*) for the simple cells (see inserted static discharge field plot). *B*: width of the non-dominant zone relative to the width of the dominant zone for the complex cells.

The width of the most responsive non-dominant zone was also measured, and expressed relative to the width of the dominant zone of the respective cell. Fig. 6*A* shows that this relative width varied between 0·4 and 1·6. The distribution was unimodal, with a mean of 0·86 (S.D. = 0·22). Accordingly, the most responsive non-dominant zone was on average 14% narrower than the dominant zone.

The distance between the position where the maximum response occurred in the dominant and in the non-dominant zone was expressed relative to the width of the dominant zone. The frequency histogram of these values was unimodal, as shown by Fig. 7*A*. The mean was 0·63 (S.D. = 0·26) which implies that the distance between the two response maxima on average was smaller than the width of the two subzones in which they occurred. This was partly due to the fact that the response maximum in the non-dominant zone usually occurred proximal to the mid point in the zone (see Fig. 3*D*), and partly due to overlap between the two zones (Fig. 3*G*).

The distance between the two response maxima increased with eccentricity in the same manner as the width of the dominant zone. The ratio between the two values

was therefore about the same at the different eccentricities studied. Also, the ratio between the width of the most responsive non-dominant zone and the width of the dominant zone was invariant over the eccentricities studied. This means that the various width aspects of the discharge field were on average magnified by the same factor with increasing eccentricity.

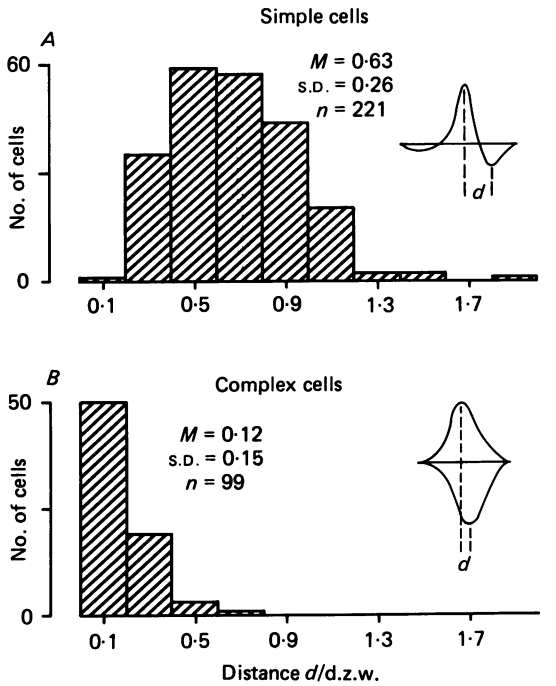

Fig. 7. Distance (d) between the position of the maximum response in the dominant zone and the position of the maximum response in the most responsive non-dominant zone expressed relative to the width of the dominant zone (d.z.w.); A: values for the simple cells; B: values for the complex cells.

Complex cells

From the static discharge field plots it was not possible to subdivide the complex cells into distinct subgroups. The discharge fields of the complex cells differed from each other partly by the smoothness of the discharge profiles, and partly by the balance of the maximum on- and the maximum off-response. Some cells had rather smooth profiles, as shown by Fig. 8A and D, but the majority had more irregular profiles with two or three peaks like the profiles in Fig. 8B and C.

Balance between on- and off-responses

The complex cells were not subdivided into distinct on- and off-dominant subtypes as were the simple cells, although the balance between the maximum on- and off-responses varied from cell to cell as illustrated by Fig. 8A and D. The frequency histogram for the ratio between the maximum off- and maximum on-response was unimodal (Fig. 2C) with a mode at 1·43. This high mode value partly reflects that

the proportion of cells with strongest on-response was larger than the proportion of cells with strongest off-response. Fig. 2 *D* shows the frequency distribution of the ratio between the maximum non-dominant and the maximum dominant response. This distribution had a mode at 0·9 and a mean of 0·72 (S.D. = 0·2). The mean non-dominant response of the complex cells was therefore 28% weaker than the mean dominant response, and this value is about half the comparable value for simple cells (57%).

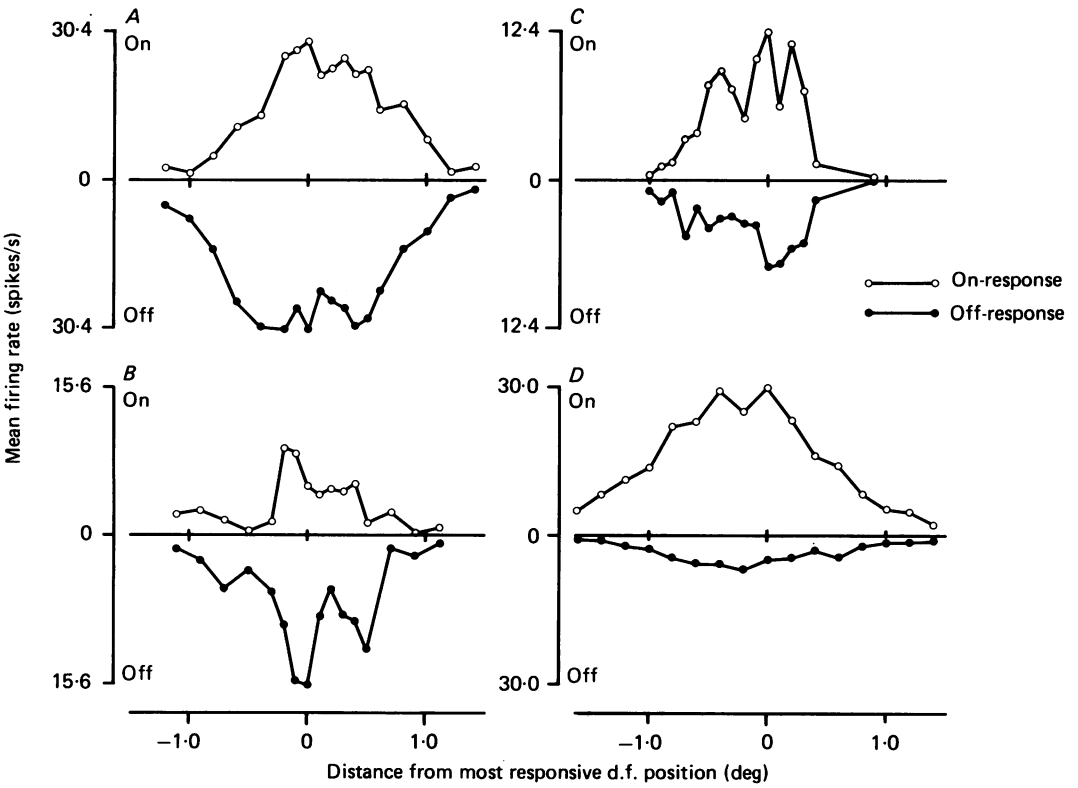

Fig. 8. Static discharge field (d.f.) plots for four complex cells made with an optimum oriented light slit flashed ten times in each of a series of positions across the discharge field. ○, mean on-response; ●, mean off-response. The on- and off-periods were 500 ms in *A–C*, and 800 ms in *D*. Slit dimensions were in *A*: 0·11 × 2·06 deg; *B*: 0·11 × 2·18 deg; *C*: 0·14 × 0·74 deg; *D*: 0·29 × 4·92 deg.

Width of the discharge field

The width of the discharge field of complex cells was not significantly different from the width of the whole discharge field of simple cells at any eccentricity as shown by Fig. 5. At the various eccentricities the mean width of the complex cell discharge field was about twice the mean width of the dominant zone of the simple cells. The width of the complex cell discharge field increased with eccentricity up to the 7·5–10 deg class and then decreased at the highest eccentricity class (Fig. 5). This low value at the highest eccentricity class could be due to sampling bias since the value was based on only twelve cells.

For almost all complex cells the on- and off-zones were about equally wide, as illustrated by Fig. 6*B*. The mean ratio between the width of the non-dominant and the dominant zone was 0·99 (S.D. = 0·08). Also, with respect to the distance between the positions where the maximum on-response and the maximum off-response occurred there was little variation among the complex cells, as illustrated by Fig. 7*B*. The mean distance was 0·12 (S.D. = 0·15), expressed relative to the width of the dominant zone.

DISCUSSION

The cells analysed in the present study fell into two distinct subgroups concerning the degree of overlap between on- and off-zones, and this parameter was used for classification into simple and complex cells. The on- and off-dominant cells formed two distinct subgroups of simple cells. Concerning the number of different discharge zones, a fifth subgroup of simple cells was distinguished in addition to the four described by Palmer & Davis (1981). All five subgroups S1–S5 occurred among the on- and the off-dominant cells. Odd and even symmetric cells (Robson, 1975) did not form distinct subgroups of simple cells. All the simple cells had asymmetric discharge field profiles, and only a very few profiles approximated the ideal even symmetric type. In contrast to this variety of simple cell subgroups, the present study failed to show distinct subgroups of complex cells with respect to the properties of the discharge field profiles.

The ratio between the maximum non-dominant and maximum dominant response for the on- and the off-dominant simple cells had almost the same frequency distribution. This shows that the various balances between on- and off-responses are represented in a complementary manner in the two subpopulations of simple cells. This supports the view that the on- and off-systems are separated in two complementary channels in striate cortex in the simple cells as a continuation of the parallel on- and off-streams at the subcortical levels.

The proportion of cells in the different subgroups S1–S4 differed somewhat from the values found by Palmer & Davis (1981). In their sample the S2 cells were most numerous, whereas in the present study S2 and S3 cells were almost equally frequent. In general, the distribution of cells in the different subgroups was shifted toward more compound fields compared to the results of Palmer & Davis (1981). This could be due to differences in the methods used in the two studies. Palmer & Davis (1981) used response planes to determine the discharge field configurations, whereas discharge field plots based on average firing rate were used in the present study. In the response planes sharp transient responses are most easily detected. Small differences in the average firing rate between different receptive field positions, which could be detected by the method used in the present study, might be more difficult to see in the response planes. Therefore the method used in the present study was probably more sensitive for detecting regions with weak and more tonic response. This difference in method could also explain, at least partly, why the complex cells with only a pure on- or a pure off-region (C1), described by Palmer & Davis (1981), were not found in the present study. Also, in the sample of Palmer & Davis (1981) this subtype was less frequent (21·8 %) than the C2 type (78·2 %) with overlapping on- and off-zones which was the only type of complex cells found in the present study.

The different configurations of on- and off-zones found in simple cells were much

less numerous than the possible combinations defined by the number of discharge zones, and two limiting conditions were identified. First, the different zones across the discharge field were alternating on- and off-zones. Secondly, the number of zones on each side of the dominant zone differed at most by one (in the S2 and S4 cells). Furthermore, the most distal zone in the S4 cells occurred on the side where the strongest non-dominant zone occurred adjacent to the dominant zone. These conditions imply that the configuration of on- and off-zones is defined for an on-dominant or an off-dominant simple cell when it is known on which side of the dominant zone the strongest response occurs. The additional variations of the fields are thereby limited to the size of the subregions, and to the responsivity in the zones. The maximum response in the various subregions decreased with the distance of the respective zone from the dominant zone, so the response pattern distally from the dominant zone looked like a damped wave-form pattern.

The different subgroups of simple cells are not necessarily produced by different types of intracortical connexions. In fact, all the different subgroups can be explained within one intracortical wiring diagram. This presumes that simple cells receive excitatory and inhibitory input only from either on- or off-centre cells of the lateral geniculate nucleus (l.g.n.), and that the excitatory and the inhibitory fields are acentric but overlapping (Heggelund, 1981*a*). On-dominant simple cells can be explained by input from on-centre l.g.n. cells, and off-dominant simple cells by input from off-centre l.g.n. cells. The discharge field profiles of the various subtypes can be derived from the model by variation of the balance between excitatory and inhibitory cortical input to the simple cell, variation of the degree of overlap between the excitatory and inhibitory field, or variation of the centre–surround balance in the receptive fields of the input fibres. This model would also explain the borderline cases between the subtypes S1–S5, and why the configurations of different on- and off-zones are so strictly limited.

Palmer & Davis (1981) found an average width of a single discharge zone of 0·92 deg (S.D. = 0·25) for S4 cells and 1·13 deg (S.D. = 0·61) for S2 cells within the central 6 deg of the visual field. This compares well with the mean width of the dominant zone of simple cells in the present study which was 1·14 deg (S.D. = 0·48) within the central 6 deg. The complex cells in the study of Palmer & Davis (1981) had somewhat wider discharge fields (mean = 3·29 deg, S.D. = 1·62) than in the present study (mean = 2·43 deg, S.D. = 0·83). Since the standard deviation of the values for the complex cells in the study of Palmer & Davis (1981) was considerably larger than in the present study, their sample probably contained more cells with very wide discharge fields. When the width of the whole discharge field of the simple cells was compared with that of complex cells, no significant difference was found in the present study.

The paracentral simple fields were like magnified central fields. The width of the dominant zone, the width of the most responsive non-dominant zone, and the distance between the positions in these two fields where the maximum response occurred, all increased in the same proportion with increasing eccentricity. Within the central 2·5 deg the width of the dominant zone varied between 0·3 and 2·1 deg. For the diameter of the receptive field centre in the retinal ganglion cells, Cleland & Levick (1974) found a range of 0·55–1·0 deg for brisk sustained cells and

1·17–2·33 deg for brisk transient cells. Peichl & Wässle (1979) found a range of 0·3–0·67 deg for brisk sustained and 0·87–1·67 deg for brisk transient cells. For cells in the l.g.n. Wilson, Rowe & Stone (1976) found a variation of centre diameters from 0·3 to 1 deg for X cells, and from 0·6 to more than 3 deg for Y and W cells, within eccentricities up to 30 deg. The width of the dominant zone in the simple cells was therefore within the widths of the receptive field centres of the retinal ganglion and l.g.n. cells. This is consistent with the model discussed above which presumes that the dominant discharge zone is produced by the receptive field centre of the input fibres, and the other subzones by the receptive field surround of the input fibres.

Complex cell discharge fields can be explained by a model (Heggelund, 1981*b*) which presumes that the excitatory and inhibitory fields have input from both on- and off-centre l.g.n. cells with overlapping receptive field centres. This means that the on- and the off-zones in these cells have a dual source of input. In the on-zone, for example, the on-response in the central part would come from the receptive field centre of the excitatory on-centre l.g.n. cells, but the on-response in the distal parts of the on-field would come from the receptive field periphery of the excitatory off-centre l.g.n. cells. It is therefore of interest to notice that the average width of the whole discharge field of complex cells differed little from that of simple cells.

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REFERENCES

ALBUS, K. (1975). A quantitative study of the projection area of the central and paracentral visual field in area 17 of the cat. I. The precision of the topography. *Experimental Brain Research* **24**, 159–179.

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

BISHOP, P. O., KOZAK, W. & VAKKUR, G. J. (1962). Some quantitative aspects of the cat's eye: axis and plane of reference, visual field co-ordinates and optics. *Journal of Physiology* **163**, 466–502.

CLELAND, B. G. & LEVICK, W. R. (1974). Brisk and sluggish concentrically organized ganglion cells in the cat's retina. *Journal of Physiology* **240**, 421–456.

HEGGELUND, P. (1981*a*). Receptive field organization of simple cells in cat striate cortex. *Experimental Brain Research* **42**, 89–98.

HEGGELUND, P. (1981*b*). Receptive field organization of complex cells in cat striate cortex. *Experimental Brain Research* **42**, 99–107.

HEGGELUND, P. (1986). Quantitative studies of enhancement and suppression zones in the receptive field of simple cells in cat striate cortex. *Journal of Physiology* **373**, 293–310.

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

LEVICK, W. R. (1972). Another tungsten electrode. *Medical and Biological Engineering* **10**, 510–515.

MOVSHON, J. A., THOMPSON, I. D. & TOLHURST, D. J. (1978). Spatial summation in the receptive fields of simple cells in cat's striate cortex. *Journal of Physiology* **283**, 53–57.

PALMER, L. A. & DAVIS, T. L. (1981). Receptive-field structure in cat striate cortex. *Journal of Neurophysiology* **46**, 260–276.

PEICHL, L. & WÄSSLE, H. (1979). Size, scatter and coverage of ganglion cell receptive field centres in the cat retina. *Journal of Physiology* **219**, 117–141.

ROBSON, J. G. (1975). Receptive fields: neural representation of the spatial and intensive attributes of the visual image. In *Handbook of Perception*, vol. V, ed. CARTERETTE, E.C. & FRIEDMAN, M. P., pp. 81–112. New York: Academic Press.

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

STEVENS, J. K. & GERSTEIN, G. L. (1976). Spatiotemporal organization of cat lateral geniculate receptive fields. *Journal of Neurophysiology* **39**, 213–238.

TOYAMA, K., KIMURA, M. & TANAKA, K. (1981). Cross-correlation analysis of interneuronal connectivity in cat visual cortex. *Journal of Neurophysiology* **46**, 191–201.

WILSON, P. D., ROWE, M. H. & STONE, J. (1976). Properties of relay cells in cat's lateral geniculate nucleus: a comparison of W-cells with X- and Y-cells. *Journal of Neurophysiology* **39**, 1193–1209.