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CORRELATION BETWEEN THE PREFERRED ORIENTATION AND SPATIAL FREQUENCY OF NEURONES IN VISUAL AREAS 17 AND 18 OF THE CAT

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SUMMARY

1. In seventy-six penetrations through areas 17 and 18 of the cat, neurones were regularly sampled at intervals of 100 μm and preferred orientation, optimal spatial frequency and resolving power were determined for each neurone in response to drifting sinusoidal gratings.

2. As already shown for area 17, in tangential penetrations through area 18, whenever the preferred orientation rotates progressively from cell to cell, the optimal spatial frequency tends to remain constant.

3. A statistical analysis on 1574 cells in areas 17 and 18 showed that for pairs of cells separated 200–300 μm along a track the difference in preferred orientation $\Delta\alpha$ and the difference in optimal spatial frequency Δf are not randomly distributed: cell pairs with small $\Delta\alpha$ are most likely to have large Δf and vice versa.

4. These findings indicate that in areas 17 and 18 neurones with the same optimal frequency are aligned along a direction orthogonal to the orientation columns.

5. The optimal spatial frequency, resolving power and the velocity cut-off were averaged for cells from different penetrations located in the same cortical layer or sublayer of area 18: mean optimal spatial frequency and acuity are highest in layer IV and lowest in layers II and V, while the velocity cut-off is highest in layers II and V and lowest in layer IV.

6. Our data suggest that the layering of cells according to optimal spatial frequency is a more subtle subdivision than the six histological layers.

INTRODUCTION

The response of visual cortical cells of the cat has been shown to be critically dependent upon some parameters of the visual stimulus such as orientation and spatial frequency.

Area 17 is known to present a highly precise cytoarchitectonic organization according to cell preferred orientation (Hubel & Wiesel, 1974; Albus, 1975). Maffei & Fiorentini (1977) have recently presented evidence for a cortical organization with respect to the cell optimal spatial frequency. Indeed, in penetrations perpendicular to the cortical surface where the cell preferred orientation tends to remain constant, there is a large spread in optimal spatial frequency, whereas in tangential penetrations,

where the preferred orientation changes regularly from cell to cell, the optimal spatial frequency tends to remain constant.

Furthermore, area 18 cells show a specificity for stimulus orientation (Hubel & Wiesel, 1965) and spatial frequency (Movshon, Thompson & Tolhurst, 1978) and a columnar organization according to preferred orientation (Hubel & Wiesel, 1965).

The aim of this work is: (1) to investigate whether area 18 presents a cytoarchitectonic organization according to optimal spatial frequency similar to area 17, and (2) to quantify the correlation between the rate of change in optimal spatial frequency and in orientation along an electrode track, for both area 17 and area 18.

METHODS

Experiments were performed on forty-three adult cats.

Anaesthesia was induced with halothane (1–2%). A small opening in the skull was made over area 17 and/or 18 and at the end of the surgical procedure all the operated areas were infiltrated with local anaesthetic (Novocaine). After removal of the dura the animal was paralysed with intravenous injection of Pavulon (Pancuronium bromide, N.V. Organon) 0·2–0·3 ml kg^{-1} h^{-1} and during the recording session anaesthesia was maintained with nitrous oxide in oxygen (70%, 30%) and supplementary sodium barbitone (5–10 mg kg^{-1} h^{-1}).

P_{CO_2} (3·8–4·2%), e.c.g. and e.e.g. were monitored throughout the experiment and the body temperature was maintained at 38 °C.

Pupils were dilated with atropine and contact lenses with artificial pupils of 3 mm diameter were applied. The refraction of the cat's eye was determined by means of retinoscopy and corrected with suitable spectacle lenses placed in front of the eye. At the beginning of the experiment the position of the papillae and of the area centralis was determined by using either an inverting ophthalmoscope or the technique described by Fernald & Chase (1971).

A micropipette filled with pontamine was inserted either perpendicularly or tangentially to the cortex and a solution of agar-agar in saline was used to prevent drying of the cortex.

The experiment began at least 2 h after the interruption of the halothane anaesthesia.

In each penetration cells were sampled regularly at intervals not greater than 100 μm. For each cell the preferred orientation, the optimal spatial frequency and the optimal drifting velocity in response to sinusoidal drifting gratings were measured either: (1) by determining the lowest contrast threshold for a number of orientations (spaced 5°), spatial frequencies (spaced 0·15–0·2 octaves) and drifting velocities (spaced 1 octave) by listening to the firing rate of the cell, or (2) by recording the average responses (or the amplitudes of response) to drifting gratings of low contrast at various orientations, spatial frequencies and drift velocities. The optimal spatial frequency could be judged with an accuracy of $\pm$0·15–0·2 octaves.

We also determined the spatial and temporal acuity of each cell (highest resolvable spatial frequency and drift velocity) using square wave gratings of the maximum available contrast. At the end of each penetration current (10–20 μA) was passed through the tip of the micropipette for 1 min; then the electrode was withdrawn at constant speed with current continuously passing. After 1 mm the withdrawal was stopped for 30 s and so on for the whole length of the track. At zero position the injection was continued for 1 min. In this way each penetration was marked with a continuous blue line with spots at every mm. At the end of the experiment the animal was perfused with 10% formaldehyde in 0·9% saline and blocks of frozen tissue were sectioned to 80 μm thickness. Sections were mounted on gelatinized slides, stained with Neutral Red and examined for the reconstruction of penetrations. For the identification of the cortical laminae we followed Gilbert (1977). Whenever necessary to assess the position of the border between area 17 and 18 we used the criteria of Movshon *et al.* (1978), based either on histological reconstruction of the traces or on the reversal of polarity of receptive field representation at the vertical meridian.

We performed altogether seventy-six penetrations, thirty-three in area 17, seventeen in area 18 in the posterolateral sulcus and twenty-six tangential to the lateral gyrus crossing the border 17–18.

We recorded from and analysed the responses of 972 cells in area 17 and 602 cells in area 18.

RESULTS

The spread of optimal spatial frequencies of cortical cells within an orientation column in area 18

As is well known, in both area 17 and area 18 of the cat all cells recorded in penetrations perpendicular to the cortical surface have their receptive fields practically superimposed and are tuned to the same or to very similar stimulus orientations (Hubel & Wiesel, 1962, 1965).

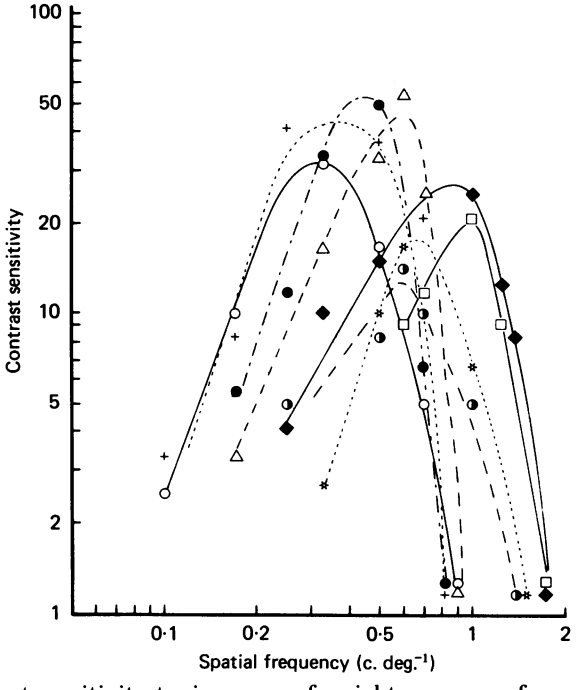

Fig. 1. Contrast sensitivity tuning curves for eight neurones of an orientation column in area 18. On the ordinate contrast sensitivity is reported on a log scale; each tuning curve was measured at the cell's optimal drifting velocity. The penetration was made perpendicularly to the cortical surface in the posterolateral gyrus and the receptive fields were within 5° of the area centralis. Histological reconstruction showed that all cells were recorded in layers IV, V, and VI. In particular, ◑, ☼, □ and ◆ were in layer IV, ○, + and △ were in layer V, and ● was in layer VI. ◑, ☼ and ◆ showed hypercomplex properties; □, +, ○ and △ were complex-like cells; ● was a simple-like cell.

In area 17, the cells of a given orientation column are not at all uniform as regards their tuning properties for the spatial frequency of sinusoidal drifting gratings: the spatial frequencies at which the various cells are tuned vary within a range as large as 2 octaves (Maffei & Fiorentini, 1977). This property is shared by area 18. Fig. 1 is a paradigmatic example of the spread of the tuning curves for cells of an orientation column in area 18. The receptive fields of these cells projected within 5° of the area centralis.

The optimal spatial frequencies of the cells of this sample are spread over a range of almost 2 octaves. This range is practically as large as the range of variation of

optimal spatial frequencies for a population of fifty-four cells in area 18 recorded by Movshon *et al.* (1978) in a number of penetrations and projecting to eccentricities up to 15°.

In area 17 Maffei & Fiorentini (1977) have found that for cells recorded in penetrations tangential to the cortex the preferred spatial frequency tends to remain constant while the orientation changes in an orderly way from cell to cell. The broad range of optimal spatial frequencies covered by cells belonging to the same orientation column in area 18 is a good basis for investigating whether area 18 is also organized in rows of constant preferred spatial frequency similar to what has been found in area 17.

We shall first report some examples of tangential penetrations through areas 18 and 17 and then a statistical analysis relating to all the cells recorded in a large number of penetrations (tangential, oblique or perpendicular to the cortical surface) in the two areas.

Optimal spatial frequency of cortical cells in tangential penetrations

Penetrations across the border between areas 17 and 18. In order to make a more direct comparison between the organization of areas 17 and 18, we made twenty-six tangential penetrations in a coronal section of the lateral gyrus passing through the border between areas 18 and 17, near Horsley-Clarke co-ordinates between P2, A2.

An example is reported in Fig. 2. As the electrode advances tangentially to the surface in area 18 the preferred cell orientation rotates gradually from vertical to horizontal. As the border is crossed, the direction of rotation reverses. The resolving power (acuity) and the optimal spatial frequency of cortical neurones also undergo a brisk change at the border between areas 17 and 18: acuity and optimal spatial frequency are much higher in 17 even if the position of the receptive fields remains the same. In the portions of the track on either side of the border, however, acuity and optimal spatial frequency are fairly constant.

The sequences of preferred orientation of the cells observed in tangential penetrations in area 18 require some additional comments. Our results, based on thirty-eight tangential penetrations in area 18, indicate that the shifts in preferred orientation along the track are less regular and predictable than in area 17. Also, the gradient of orientation with respect to track distance is different in the two areas. The average rate of change in preferred orientation in tangential tracks through area 18 is 110–130° mm^{-1} and the largest value we observed was 150° mm^{-1}. In area 17 (in agreement with Albus, 1975; I. D. Thompson & D. J. Tolhurst, in preparation) the orientation gradient is of the order of 180–220° mm^{-1} (see Figs. 2 and 4). This could indicate that the orientation columns are somewhat larger in area 18 than in area 17, at least along the direction tested in our coronal penetrations.

Tangential penetrations in area 18. Ten penetrations have been performed in a coronal section of the posterolateral sulcus, near the projection of the area centralis.

Fig. 3 shows the results for one of these penetrations. As the micro-electrode advances for $\frac{1}{2}$ mm the preferred orientation shifts gradually, while the cell resolving power and optimal spatial frequency remain fairly constant. As the micro-electrode progresses further for $\frac{1}{4}$ mm the orientation remains fairly constant, while the resolving power and optimal spatial frequency tend to vary. Then there is a reversal

in the rotation of orientation and an orientation shift for a further $\frac{1}{2}$ mm accompanied by small random variations of resolving power and preferred spatial frequency. Finally (three to four neurones) the orientation tends again to be constant while the resolving power and optimal spatial frequency vary.

It is of interest to note that the first nine cells of this penetration, in addition to being tuned to similar spatial frequencies, also shared other response properties: all

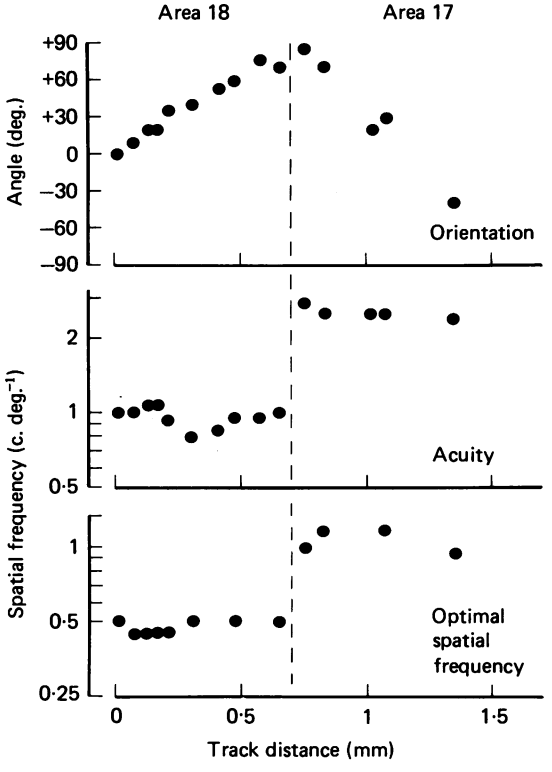

Fig. 2. Response properties of cells recorded in a tangential penetration through area 18 and 17. The preferred orientation (top), the resolving power (middle) and the optimal spatial frequency (bottom) of fifteen neurones recorded in a penetration straddling the 18–17 border are plotted against track distance. The penetration was made in the right hemisphere, moving from lateral to medial. The position of the border between area 18 and 17 was estimated on the basis of receptive field projection (see Methods).

these cells responded only to simultaneous stimulation of both eyes and their discharge was clearly modulated by the single bars of the grating (for other details see caption). In area 18 it is not rare to encounter cells which respond only to simultaneous stimulation of both eyes: forty-six out of 602 cells in our sampling were of this type and 80% of these were found in the deeper part of layer III.

As it is shown in the histological reconstruction of this penetration, the initial part of the penetration is in layer III and the termination in layer IV. In the portion of the track where the electrode passed from layer III to layer IV there is a flattening followed by a reversal in the curve of orientation *vs.* track distance (Fig. 3), and also

an increase in cell resolving power and optimal spatial frequency. This was a common finding in both areas 17 and 18, where the majority (eight out of ten in area 17 and eight out of nine in area 18) of reversals or discontinuities in the sequence of preferred cell orientation *vs.* track distance coincides with step-wise changes in optimal spatial frequency (and acuity) of the cells. Discontinuities in the sequence of preferred orientation and spatial frequency, however, do not necessarily occur only when the electrode passes from one layer to the next one. They also occur within a single layer (see Fig. 4).

Tangential penetrations in area 17. In addition to the twenty-six penetrations mentioned above which straddled the border between areas 18 and 17, twenty-five tangential penetrations were confined to area 17, in the medial bank of the lateral gyrus (P4–6). The results of one of these penetrations are reported in Fig. 4. All the cells were recorded in layer VI.

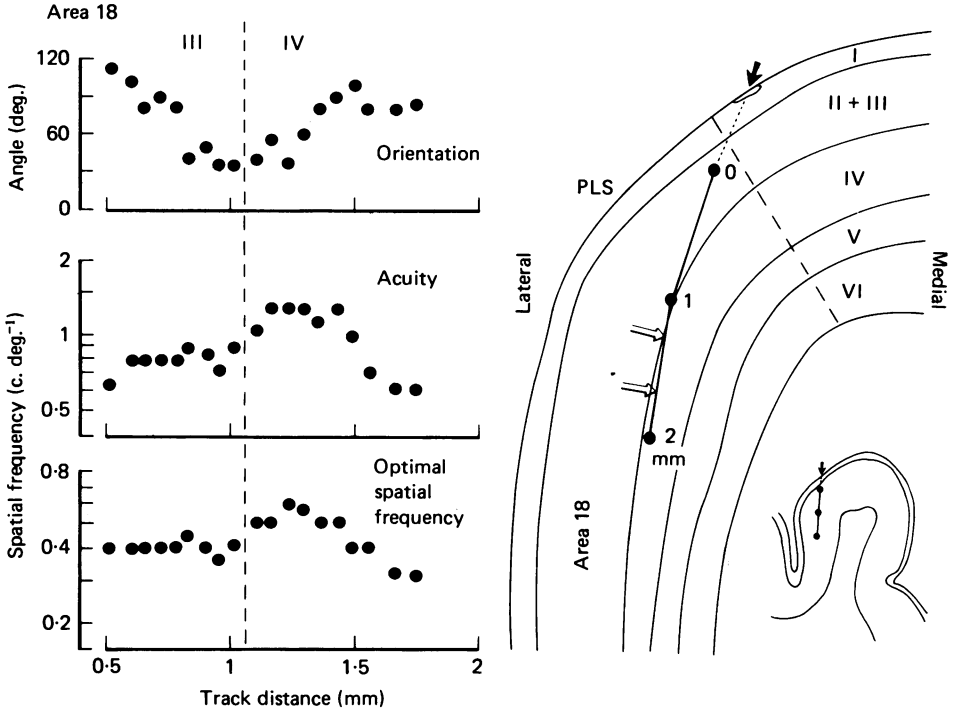

Fig. 3. Tangential penetration in area 18. The response properties of cells recorded in a tangential penetration down the posterolateral sulcus (PLS) are plotted against track distance. The histological reconstruction shows that the electrode travelled through layers III and IV, crossing the III–IV border at about 1 mm from the beginning of the track. All cells recorded in layer III were driven only by the simultaneous stimulation of both eyes, had the same cut-off velocity (20–25° s^{-1}), and their response was modulated by the single bars of the drifting grating. Cells recorded in layer IV were driven mainly by the contralateral eye (right eye).

The black arrow in the histological reconstruction marks the entrance of the micropipette. The black dots along the track are the sites of the pontamine injections made by stopping the electrode during withdrawal; between dots, current was continuously passed through the tip (continuous line, for other details see Methods). The white arrows indicate the portion of the penetration shown in Plate 1. The smaller magnification drawing shows the position of the track with respect to the mid line and the posterolateral sulcus.

The preferred orientation varies continuously along the track but shows at least two reversals, while the cell optimal spatial frequency presents a distribution with two plateaux. The two groups of cells with different preferred spatial frequencies are located at different depths in layer VI. The sudden change in optimal spatial frequency possibly coincides with the electrode entering a deeper sublayer of layer VI.

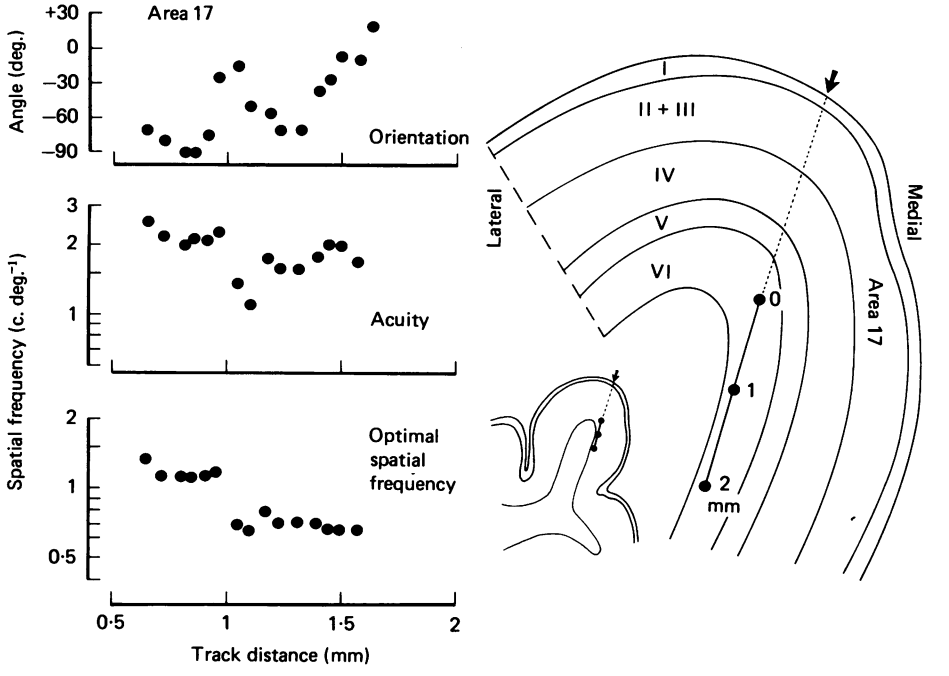

Fig. 4. Tangential penetration in area 17. Abscissa and ordinate same as in Fig. 2. The penetration was made vertically in the medial bank of the left lateral gyrus. The histological reconstruction shows that the track was entirely in layer VI. The jump in preferred orientation, resolving power and optimal spatial frequency is well in accordance with the electrode passing from a medial to a deeper part of layer VI. All cells up to 1 mm had a non-modulated response and cut-off velocity below 5° s^{-1}; cells beyond 1 mm clearly modulated their firing rate and their cut-off velocity was about 10–20° s^{-1}.

Correlation between preferred orientation and optimal spatial frequency

In this section we present the results of a statistical analysis of the whole set of cells recorded in all penetrations perpendicular, tangential and oblique to the cortical surface. We have looked for a correlation between variations in preferred orientation and in optimal spatial frequency from cell to cell along a track. The total number of cells examined is 1574. The analysis has been made separately for area 17 (972 cells) and area 18 (602 cells). In each penetration we considered all possible pairs of cells such that the second cell was separated 200–300 μm from the first along the electrode track. This rather large spacing has been chosen to avoid comparing the parameters of pairs of cells too close to each other (in a range of 100 μm) for which Thompson & Tolhurst (1980*a*) have already shown that the optimal spatial frequencies are statistically very similar. For each pair of cells we evaluated the difference $\Delta\alpha$ in the preferred orientations of the two cells ($0° \leqslant \Delta\alpha \leqslant 90°$) and the difference Δf (in

octaves) in their preferred spatial frequencies. The values of $\Delta\alpha$ and Δf for each pair of cells have been reported in a $\Delta\alpha$, Δf plane. If the two variables $\Delta\alpha$ and Δf were independent of each other, the pairs of cells would have been uniformly distributed in the $\Delta\alpha$, Δf plane.

The density distribution actually observed in area 17 is shown in Fig. 5. The distribution covers a roughly triangular area with most cell pairs with large

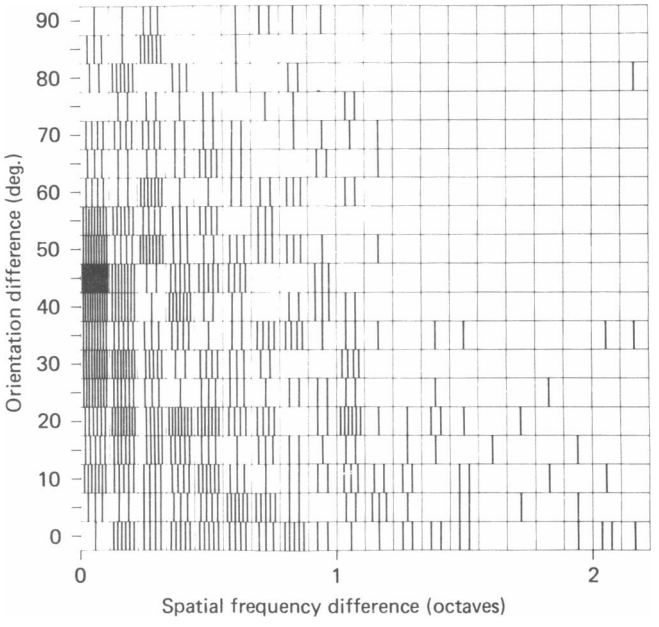

Fig. 5. Density distribution of cell pairs recorded 200–300 μm apart, in the $\Delta\alpha$–Δf plane for area 17. The difference $\Delta\alpha$ in optimal orientation is reported on the ordinate, the difference Δf in optimal spatial frequency is reported on the abscissa. Each line represents a cell pair. Total number of cell pairs, 599.

differences in preferred spatial frequency ($\Delta f > 1$ octave) confined in the region of small $\Delta\alpha$ and most cell pairs with relatively large differences in preferred orientation ($\Delta\alpha = 40$–$60°$) confined in the region of small Δf. Moreover, the density of the distribution is relatively low in the left-hand corner of the graph: cell pairs with the same preferred orientation *and* the same preferred spatial frequency are relatively infrequent.

This is better illustrated by the graphs of Fig. 6 that display the distribution of subpopulations of cell pairs extracted from the whole population of Fig. 5. First two subpopulations were selected consisting of all cell pairs with Δf less than 0·2 octaves and Δf greater than 1 octave, respectively. Fig. 6*A* shows how the cell pairs of the two subpopulations are distributed in terms of their difference in preferred orientation, $\Delta\alpha$. The frequency distributions of the two subpopulations are clearly different and almost mirror images of each other: one of them ($\Delta f < 0{\cdot}2$ octaves) has a peak for values of $\Delta\alpha$ between 40 and 60° (crosses and solid line) while the peak of the other distribution ($\Delta f > 1$ octave) corresponds to the smallest values of $\Delta\alpha$ (open circles and dashed line).

Note that a change of 40–60° in 200–300 μm corresponds to the mean rate at which the preferred orientation of cells in area 17 rotates along penetrations tangential to the cortical surface (200° mm^{-1}, Albus, 1975; I. D. Thompson & D. J. Tolhurst, in preparation). Conversely, the pairs of cells with $\Delta\alpha$ close to zero are likely to belong to the same orientation column. The frequency distributions of Fig. 6*A*, therefore, can be interpreted as showing that the probability for two cortical cells separated 200–300 μm from each other to be tuned to the same spatial frequency is highest when the two cells are aligned along a direction perpendicular to the orientation slabs and is lowest when the two cells belong to the same orientation slab.

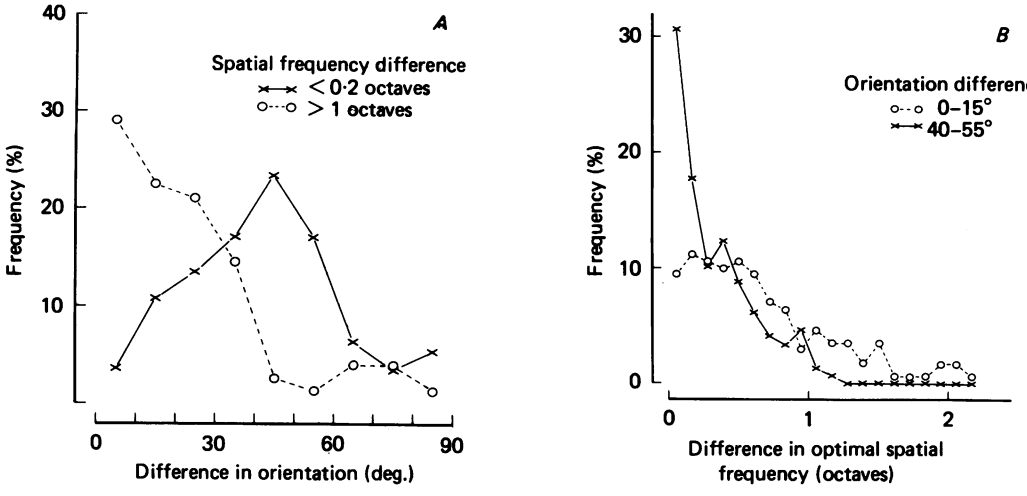

Fig. 6. Area 17. *A*, frequency distributions for two populations of cell pairs having a difference in optimal spatial frequency (Δf) either below 0·2 or above 1 octave, with respect to their difference in preferred orientation ($\Delta\alpha$). On the abscissa the difference in preferred orientation ($\Delta\alpha$) varies in steps of 10°. Open circles, dashed line: $\Delta f > 1$ octave, total number of cell pairs $n = 76$. Crosses, continuous line: $\Delta f < 0{\cdot}2$ octaves, $n = 112$. *B*, frequency distributions for two populations of cell pairs having a difference in preferred orientation ($\Delta\alpha$) either between 0 and 15° or between 40 and 55°, with respect to their difference in optimal spatial frequency (Δf). Open circles, dashed line: $0° \leqslant \Delta\alpha \leqslant 15°$, $n = 169$. Crosses, continuous: $40° \leqslant \Delta\alpha \leqslant 55°$, $n = 147$.

The minority of cell pairs with $\Delta\alpha > 60°$ probably reflects the step-wise changes in preferred orientation observed occasionally in some penetrations.

A complementary analysis was then performed by sampling out from the total population of the cell pairs of Fig. 5 two subpopulations consisting of cell pairs either with a small difference in preferred orientation ($\Delta\alpha \leqslant 15°$) or with a difference around 50° ($40° \leqslant \Delta\alpha \leqslant 55°$). The frequency distributions of these two subpopulations with respect to their Δf values (Fig. 6*B*) show that a large proportion of the pairs of cells with $\Delta\alpha = 50°$ have little or no difference in preferred spatial frequency. Conversely, pairs of cells differing in orientation 0–15° show a large spectrum of differences in optimal spatial frequency. Indeed, for one-third of these cell pairs Δf is greater than 1 octave.

These findings are in agreement with and extend the previous ones in that for small differences in preferred orientation there is a large spread in optimal spatial

frequency, whereas for large variations in preferred orientation, the spread of Δf differences is much smaller (30·6 % of the pairs of cells show the same preferred spatial frequency).

Evidence that the width of the regions of constant spatial frequency tuning is small in the direction orthogonal to the cortical surface comes from a further statistical analysis performed separately for cell pairs recorded along tracks perpendicular, oblique or tangential to the cortical surface (Table 1).

The tracks were classified into three classes according to their prevailing orientation with respect to the cortical layers, as shown by their histological reconstruction. The majority of penetrations classified as oblique made an angle of more than 45° with the direction perpendicular to the cortical surface.

TABLE 1. Percentages of cell pairs with different $\Delta\alpha$ or Δf in perpendicular, oblique and tangential penetrations in area 17

	Cell pairs	$\Delta\alpha \leqslant 20°$ (%)	$\Delta\alpha > 20°$ (%)	$\Delta f < 0{\cdot}3$ (%)	$0{\cdot}3 \leqslant \Delta f \leqslant 1$ (%)	$\Delta f > 1$ (%)
Perpendicular penetrations	105	78	22	19	45·7	35·3
Oblique penetrations	159	37	63	45·3	43·4	11·3
Tangential penetrations	335	25·6	74·4	55·4	40·8	3·8

The differences between the distributions of cell pairs across the various intervals for the three classes of penetrations is highly significant ($P < 10^{-6}$, χ^2 test).

As expected from the previous considerations of the overall statistics, a large proportion (35 %) of cell pairs recorded in a direction perpendicular to the cortical surface have $\Delta f > 1$ octave. For tangential penetrations this percentage is only 4 %. Conversely, the proportion of cell pairs with $\Delta f < 0{\cdot}3$ octaves is 55 % for tangential penetrations and only 19 % for penetrations perpendicular to the cortical surface. The percentages for the oblique penetrations are intermediate between the previous ones, but relatively closer to those for the tangential penetrations as expected from the orientation of the majority of them.

A similar analysis was performed in area 18. From all tracks tangential, oblique or perpendicular to the cortical surface all cells were selected that were separated 200–300 μm from each other and every such cell pair was labelled with the cell difference in preferred orientation, $\Delta\alpha$ and in optimal spatial frequency, Δf. The resulting density distribution is very similar to that shown in Fig. 5 for area 17, except that cell pairs with small Δf are grouped between 20–40°.

Two subpopulations of cell pairs were then selected with Δf less than 0·2 octaves and greater than 0·5 octaves, respectively. The lower limit of the second subpopulation was set at 0·5 octaves rather than 1 octave, as for area 17, because the cell pairs with very large Δf were not numerous enough in our population for area 18.

Fig. 7*A* shows the frequency distribution of the two subpopulations with respect to the difference in preferred orientation.

The peak of the distribution with $\Delta f < 0{\cdot}2$ octaves (crosses and continuous lines)

corresponds to classes of cell pairs with $\Delta\alpha$ in the range 20–35°. For a cell separation of 200–300 μm, this corresponds to an average rate of change in preferred cell orientation of about 110° mm^{-1}, that is, typical of tangential penetrations through area 18 (see above). (Note that the peak in the corresponding distribution of Fig. 6*A* for area 17 corresponds to a higher value of $\Delta\alpha$, in agreement with the higher rate of change of preferred cell orientation in tangential penetrations in area 17).

The distribution of all pairs with Δf greater than 0·5 octaves (circles and dashed line in Fig. 7*A*) peaks for the class of cell pairs with the smallest values of $\Delta\alpha$, similar to what occurs in the corresponding distribution for area 17.

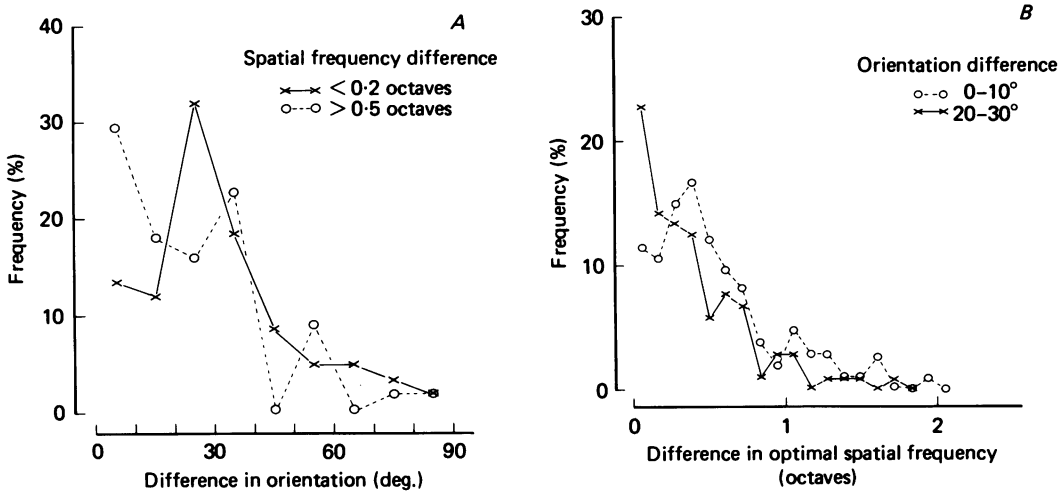

Fig. 7. Area 18. *A*, frequency distributions for two populations of cell pairs having a difference in optimal spatial frequency (Δf) either below 0·2 or above 0·5 octaves, with respect to their difference in preferred orientation ($\Delta\alpha$). On the abscissa the difference in preferred orientation ($\Delta\alpha$) varies in steps of 10°. Open circles, dashed line: $\Delta f > 0{\cdot}5$ octave, total number of cell pairs, $n = 44$. Crosses, continuous line: $\Delta f < 0{\cdot}2$ octaves, $n = 59$. *B*, frequency distributions for two populations of cell pairs, having a difference in preferred orientation ($\Delta\alpha$) either between 0 and 10° or between 20 and 30° with respect to their difference in optimal spatial frequency (Δf). Open circles, dashed line: $0° \leqslant \Delta\alpha \leqslant 10°$, $n = 104$. Crosses, continuous line: $20° \leqslant \Delta\alpha \leqslant 30°$, $n = 105$.

We then selected two other subpopulations of cell pairs for which $\Delta\alpha$ was between 0 and 10° and 20 and 30°, respectively. The frequency distributions of these cell pairs with respect to their Δf values are shown in Fig. 7*B*. Note that the classes of cell pairs with the smallest values of Δf are more numerous in the subpopulation with $\Delta\alpha$ between 20 and 30° (crosses and continuous line) than in the population with $\Delta\alpha$ between 0 and 10°, while the opposite is true for the classes of cell pairs with larger Δf values.

The results of Fig. 7 are in qualitative agreement with those of Fig. 6 if one takes into account the different rates at which orientation changes in area 18 as compared with area 17, when the electrode moves parallel to the cortical surface. The two Figures clearly indicate that the two quantities $\Delta\alpha$ and Δf are not independent of each other and confirm the observation that in penetrations in which the orientation tends to

remain constant from cell to cell, the optimal spatial frequency is more likely to vary within a large range, whereas in tracks in which the orientation changes regularly at a high rate, the optimal spatial frequency is more likely to remain constant. It should be noted however that the correlation between $\Delta\alpha$ and Δf is stronger in area 17 than in area 18.

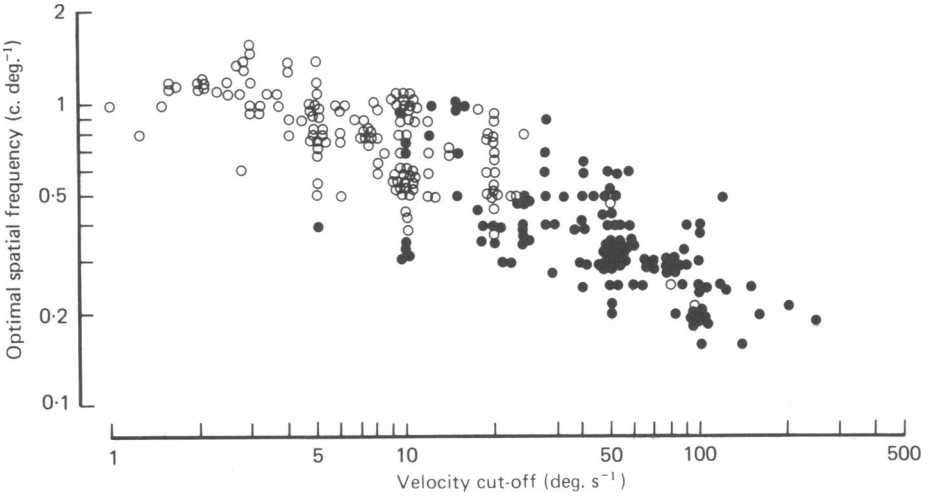

Fig. 8. Correlation between cut-off velocity and optimal spatial frequency for cells in areas 17 (open circles) and 18 (filled circles).

Mean resolving power, optimal spatial frequency and velocity cut-off of cells in the various cortical layers

The large sample of cells recorded and a careful histological reconstruction of the microelectrode penetrations have made it possible to infer the mean distribution of the spatial characteristics of cell response in the various cortical layers. The averaged data clearly show that the highest values of optimal spatial frequency and acuity are obtained in the deeper portion of layer IV and the lowest values in layers II and V. The opposite is true for another parameter of the cell response, i.e. the highest velocity of a drifting grating at which the cell responds: most of the cells that respond to the highest stimulus velocities are located in layer II and V and most cells with low velocity cut-off are in layer IV. This suggests a possible negative correlation between optimal spatial frequency and velocity cut-off, a fact that was confirmed by an analysis on a large population of cells of areas 17 and 18.

Fig. 8 illustrates this finding. Clearly the cells tuned at higher spatial frequencies tend to have lower velocity cut-off and vice versa. The populations of cells of the two cortical areas show little overlap, at least as regards the velocity cut-off; the distribution of area 18 cells can be regarded as the continuation of the distribution of area 17 (see also Orban, Kennedy & Maes, 1981).

An example of how the various parameters of the cell responses vary through the cortical layers is best supplied by an oblique penetration. One of them is illustrated in Fig. 9. This penetration was in the posterolateral sulcus. The recording began in the superficial part of layer III and continued in the deeper part of the same layer. The electrode then passed obliquely through layers IV, V and VI. At the beginning

of the recording, the penetration is approximately parallel to the interlayer surface. The results show a regular variation of the preferred orientation of the cells while the optimal spatial frequency remains fairly constant. When the electrode penetrates more obliquely into the deeper part of layer III, there is a step-wise change in the orientation sequence and an increase in optimal spatial frequency. Subsequently the micro-electrode enters obliquely into layer IV. There is another sudden change in

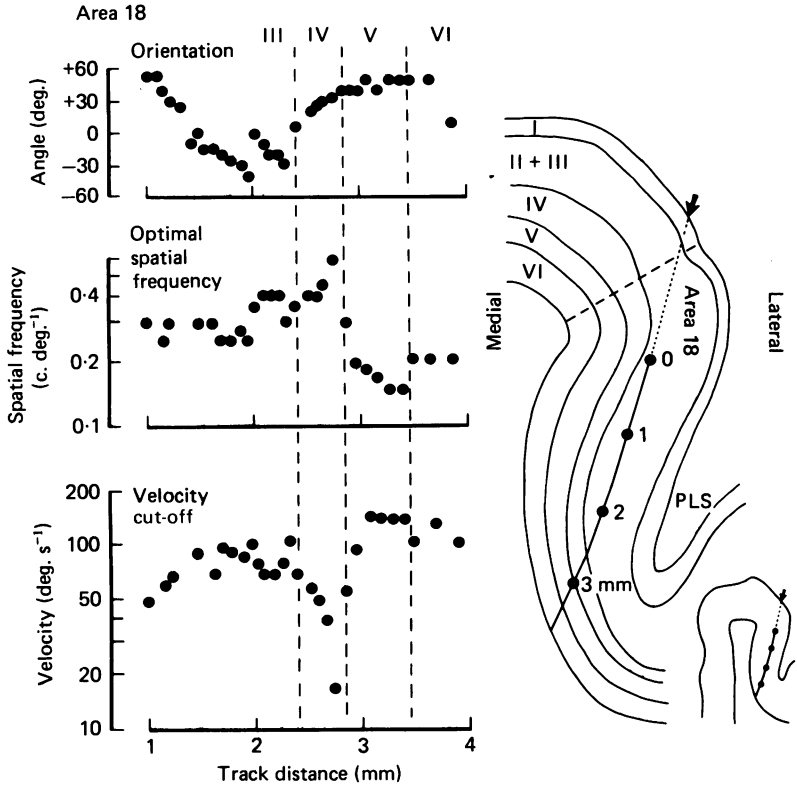

Fig. 9. Oblique penetration in area 18. The penetration was made down the medial bank of the posterolateral gyrus, in the right hemisphere. The histological reconstruction shows that the electrode advanced for a fairly long distance within layer III, and then traversed layers IV, V and VI. The majority of cells in layer III were activated only by the simultaneous stimulation of both eyes; the cells in layer IV were activated only by the ipsilateral eye, and two of them were inhibited by the contralateral eye; the cells in layer V were binocularly driven and their discharge was modulated up to 100 Hz.

orientation accompanied by a further increase in optimal spatial frequency. Then the orientation remains constant up to the end of the penetration while the optimal spatial frequency shows scattered values. The passage from layer IV to layer V is accompanied by a decrease in optimal spatial frequency. The velocity cut-off passes from a rather high mean value (60–70° s^{-1}) in layer III to a minimum (15° s^{-1}) in layer IV and a maximum (150–160° s^{-1}) in layer V and VI.

This track supplies a further example of how the spatial tuning characteristics of the cells may be different at different depths within the same cortical layer (see also Fig. 4).

DISCUSSION

The present findings are based on a large population of cells recorded in penetrations oriented at various angles with respect to the cortical surface in both areas 17 and 18 of the cat. A crucial point for the interpretation of these findings is the regular sampling of the cells at 100 μm intervals. The results of the physiological and histological analysis suggest that the cortical areas 17 and 18 present an orthogonal cytoarchitectonic organization with respect to the two parameters that optimize the cell response, i.e. the orientation and spatial frequency of the stimulus. Whenever the preferred orientation changes progressively from cell to cell as may occur in tangential penetrations, the preferred spatial frequency tends to remain constant for considerable portions of the track. Conversely, whenever the preferred orientation remains constant from cell to cell, as may occur in perpendicular penetrations, the preferred spatial frequency tends to show more frequent and substantial variations along the track.

This suggestion is supported by the statistical analysis of our data that disregards information derived from the histological reconstruction of the tracks. The density distribution of pairs of cells at 200–300 μm intervals shows that large differences (40–60° in area 17) in orientation preference are most likely to be accompanied by small changes in preferred spatial frequency whereas the reverse is true for small changes in orientation preference (Figs. 5 and 6). On the other hand, pairs of cells having the same preferred orientation *and* the same preferred spatial frequency are relatively rare, even if the population of cell pairs was collected from a large variety of tracks at different angles of penetration.

Moreover, the statistics that take into account the histological reconstruction of the tracks show that the probability of finding large changes in optimal spatial frequency is largest for cells recorded along penetrations perpendicular to the cortical surface and smallest for tangential tracks. All this is in favour of an organization of cells with the same preferred spatial frequency perpendicular to the orientation columns.

It has to be expected that sequences of cells with the same preferred spatial frequency have a limited extent, since, on the average, the optimal spatial frequency decreases from the centre to the periphery of the cortical projection of the visual field. In fact, our longest sequences of cells with constant spatial frequency in area 17 are of the order of 800–900 μm. Whether the extension of these sequences is comparable in two orthogonal directions tangential to the cortical surface we cannot say. The sampling of cells along any penetration is not frequent enough to evaluate accurately how far the preferred spatial frequency remains constant along a direction perpendicular to the cortical surface. However, our data from oblique penetrations provide evidence that the layering of cells according to preferred spatial frequency is a more subtle subdivision than the six histological layers.

It is interesting to note that within each sublayer where cells tend to be homogeneous with respect to spatial frequency tuning, they are also homogeneous with respect to all the other physiological parameters we have tested (cell type, pattern of response to drifting gratings, temporal characteristics, spatial frequency bandwith).

Recently, physiological and histochemical findings have been reported that seem to contradict ours. We think, however, that the disagreement is only apparent.

(*a*) Thompson & Tolhurst (1980*a*) report a statistical analysis on the difference in preferred spatial frequency of pairs of cells recorded in the same penetration at 0–100 or 250–500 μm interdistance. They claim that the difference in preferred spatial frequency of the cell pairs with a separation more than 250 μm varies in a wide range. This finding does not contradict ours, since Thompson & Tolhurst did not take into consideration the difference in preferred orientation of the cells of each pair. In a more recent work I. D. Thompson & D. J. Tolhurst (in preparation) present the sequences of preferred spatial frequencies for two oblique penetrations and claim that the preferred spatial frequency varies along these tracks as much as or more than along perpendicular penetrations. The change in preferred orientation of the cells is not reported in their figures and it is impossible therefore to establish whether and how the variations in preferred spatial frequency are correlated with changes in preferred orientation. We have a number of examples of tangential tracks (for instance Fig. 3) where optimal spatial frequency changes are observed in sequences of cells wherever orientation changes irregularly or does not change at all. This may occur for cells that according to the histological reconstruction belong to the same lamina. In fact the statistical analysis of Thompson & Tolhurst on their data does not contradict our findings.

(*b*) By the [^{14}C]2-deoxyglucose technique Thompson & Tolhurst (1980*b*) and Silverman, Tootell & De Valois (1980) failed to find evidence for spatial frequency rows in area 17. Rather, their data seem to imply a columnar organization with respect to the spatial frequency tuning of the cells, although neither group specifically stated that they had evidence for spatial frequency columns.

It has to be noted, however, that the deoxyglucose technique has only a limited resolution. The orientation columns obtained in the cat with this technique (Albus, 1979) have a width (400 μm) that greatly exceeds the width estimated from electrophysiological data. Because of this poor resolution it may be impossible to reveal grouping of cells with different optimal spatial frequency because of: (1) the partial overlapping of the tuning curves of cells tuned to different spatial frequencies, and (2) the columnar organization of inhibitory terminations in layers II and III (A. Hendrickson, personal communication). The activation of inhibitory pathways gives positive results with the [^{14}C]2-deoxyglucose technique.

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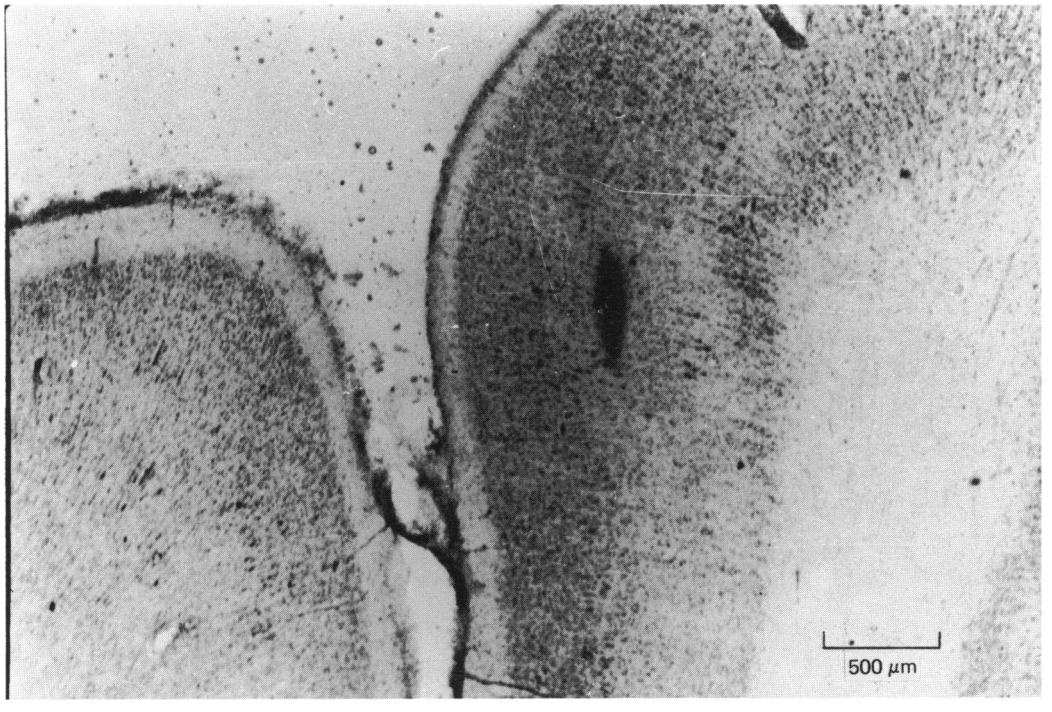
EXPLANATION OF PLATE

Neutral Red stained section showing the part of the penetration illustrated in Fig. 3 which is between the two white arrows.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