

SHAPE AND ARRANGEMENT OF COLUMNS IN CAT'S STRIATE CORTEX

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Cells in the cat's striate cortex show marked specificity in their responses to restricted retinal stimulation (Hubel & Wiesel, 1959, 1962). The most effective stimulus shapes are long narrow rectangles of light ('slits'), dark bars against a light background ('dark bars'), and straight-line borders separating areas of different brightness ('edges'). A given cell responds vigorously when an appropriate stimulus is shone on the receptive field or moved across it, provided the stimulus is presented in a specific orientation. This orientation is termed the 'receptive-field axis orientation'. It is critical, and constant for any particular cell, but may differ for different cells.

The visual cortex is subdivided into discrete regions or columns extending from surface to white matter, in which all cells have the same receptive-field axis orientation (Hubel & Wiesel, 1962). The present experiments were undertaken with the object of learning more about the anatomical configuration of the columns. We wished to have a clearer idea of their shape, especially if the walls of a column were, as previous work suggested, parallel to the radial fibre bundles of the cortex and perpendicular to the cortical layers, and whether the columns were uniform or irregular in their cross-sectional shape and size. Furthermore, we were curious to know if there was any relationship between the receptive-field axis orientations of neighbouring columns, or whether, on the contrary, the different columns were intermixed in a random way throughout the cortex.

These questions were approached: (1) by making several deep, closely spaced, parallel micro-electrode penetrations, placing electrolytic lesions at every shift in receptive-field orientation, and (2) by making many short penetrations in a small cortical area, noting the axis orientation of cells lying in the upper one or two layers of cortex.

METHODS

Seven cats were used. Projection techniques for retinal stimulation, and general procedures for preparing the animal, including anaesthesia, immobilization of the eyes, correction of refractive errors, and mapping of area centralis and optic disks on the projection

screen, have been described elsewhere (Hubel & Wiesel, 1959, 1960, 1961, 1962). Recordings were made with tungsten micro-electrodes (Hubel, 1957). Electrode tip positions were marked by making electrolytic lesions (Hubel, 1959). In order to see the surface of the cortex and to vary the point of entry of the electrode we have used a closed-chamber system similar to that described by Davies (1956). The micro-electrode was advanced by a hydraulic system instead of a machine screw, and provision was made for varying the angle between the electrode track and the cortical surface. Before the lid was placed on the chamber the surface of the cortex was photographed through a dissecting microscope and an enlarged print was made. Points of entry of the electrode relative to cortical blood vessels were indicated on this map (Pl. 1, 2). At the end of the experiment the calvarium was removed and the brain photographed again, in order to locate on its surface the position of the small area studied. Animals were perfused with 10 % formalin, and all brains were subsequently examined histologically.

RESULTS

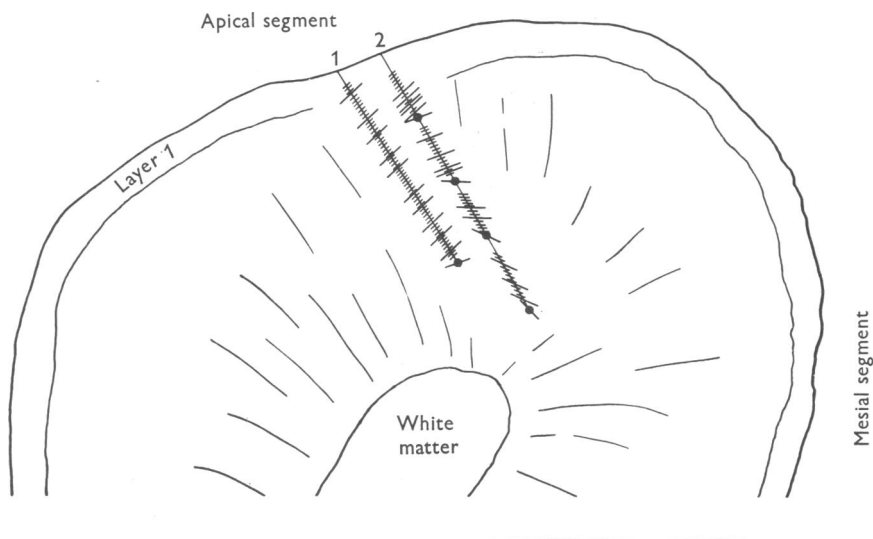
Mapping of columnar walls

Previous experiments involving single penetrations through cortical grey matter suggested that the walls of a column were perpendicular to the cortical layers and parallel to the radial fibre bundles (Hubel & Wiesel, 1962). The evidence for this was the long distance between shifts in receptive-field axis orientation in penetrations perpendicular to the layers, as opposed to the much shorter distances seen in tangential penetrations. In the present study we have sought further evidence by making in the same experiment two or more closely spaced parallel penetrations, marking the point of each shift of axis orientation with an electrolytic lesion. In all experiments to be described in this paper recordings were made in the part of the cortex that receives projections from the area centralis of the retina.

A reconstruction of two parallel penetrations made about 175μ apart is shown in Text-fig. 1. Penetration 1 was for some distance almost parallel to the fibre bundles. Penetration 2 soon became oblique, and was finally almost tangential to the cortical layers. The receptive-field orientation of the first cells recorded was the same for the two penetrations; and when the orientation in each changed the two new orientations were again identical. The points of transition are shown by the only lesion in penetration 1 and by the most superficial in penetration 2. Although these points are far apart, it will be seen that one is almost directly above the other, i.e. they lie on a line that is nearly parallel to the radial fibre bundles.

In the experiment of Text-fig. 2 six parallel penetrations were made in the same coronal plane, approximately 100μ apart. Thirty-five cells were isolated and studied, and throughout each penetration unresolved background activity gave continuous information on the receptive-field orientation. In penetrations 2-5, a 10 o'clock-4 o'clock orientation was found from the outset, and each penetration was discontinued as soon as this orientation changed. Different orientations were found from the start in penetrations 1 and 6. The approximate extent of one column in this plane

is therefore indicated by the extent of penetrations 2-5. The 2.30-8.30 orientation noted in penetration 1 and at the terminations of penetrations 2-4 must represent the column just lateral (to the left in the figure) to the one mapped, while the 2.00-8.00 orientation of penetration 6 presumably represents the column just medial to it. As in the previous experiment, the points of transition marked by the deepest extent of penetrations 2-5 seem to lie along a line that is parallel to the radial lines of the cortex.

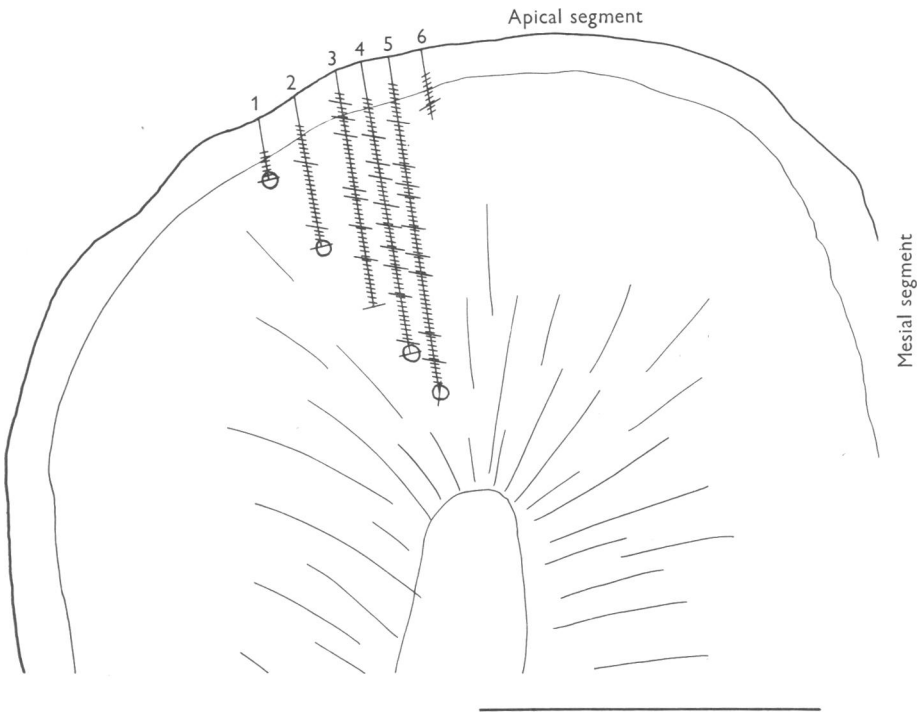


Text-fig. 1. Reconstruction of two parallel micro-electrode penetrations in the anterior part of the post-lateral gyrus. Longer lines intersecting the electrode tracks represent cortical cells. Receptive-field axis orientations are shown by the directions of these lines; lines perpendicular to tracks represent horizontal orientation. Shorter lines represent regions in which unresolved background activity was observed. Electrolytic lesions were made at every change of receptive-field orientation; these are indicated by filled circles. Scale, 1 mm.

As might be expected, the deepest penetration (No. 5) is the one that comes closest to being parallel to the radial lines throughout its extent. In this plane of section the column may not reach white matter, perhaps because the plane of penetrations intersects the anterior or posterior wall of the column. The 1.00-7.00 orientation at the end of penetration 5 may thus represent the column in front of or behind the one mapped.

In the apical segment of the post-lateral gyrus the radial lines converge with increasing depth, and the columns may thus be very narrow near the white matter. The fact that 'pure' penetrations, those extending from surface to white matter without change in orientation, have been relatively rare is therefore not surprising. At present it therefore seems likely that

all columns extend through the entire thickness of the cortical grey matter.



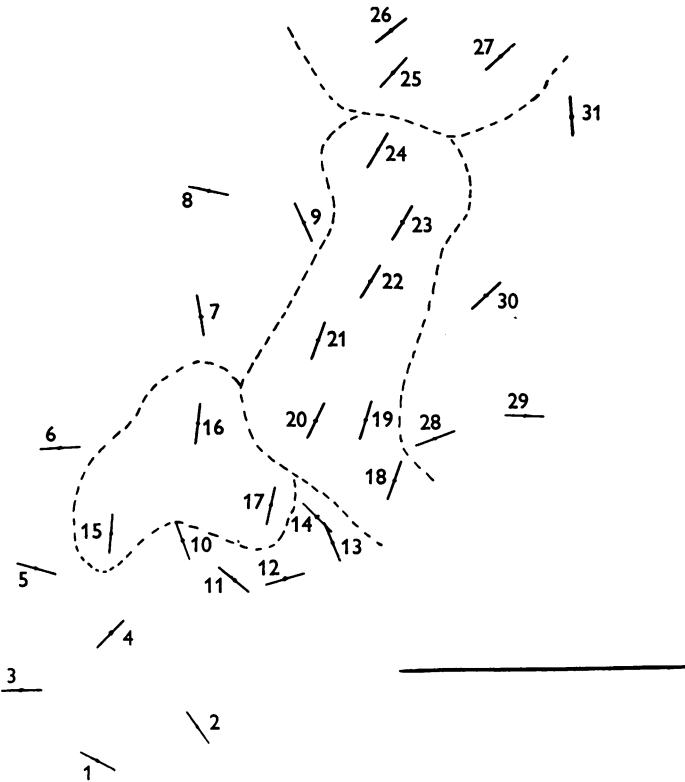
Text-fig. 2. Reconstructions of six micro-electrode penetrations in the apical segment of post-lateral gyrus near its anterior end. Open circles represent electrolytic lesions. Other conventions as in Text-fig. 1. Scale, 1 mm.

Surface mapping

Several experiments were done with the object of mapping on the cortical surface one or two columns as completely as possible. For a number of reasons this was not easy. Since one penetration took 15–20 min to complete, the total number of penetrations in a single experiment was limited. Penetrations could not be spaced closer than about 50μ , a distance which, as it turned out, was none too small for delineating the smallest columns. Finally, receptive-field orientations could be estimated only to within $5\text{--}10^\circ$, an error which was not important when two neighbouring columns differed in orientation by more than about 20° , but which led to some difficulties in defining the exact borders of a column if the difference was smaller than that.

Text-figure 3 and Pl. 1 show a map, based on 31 penetrations, of a region of striate cortex measuring about 1×3 mm. Within this area there

is a suggestion of three columns, which have been partially outlined by interrupted lines. This experiment and other similar ones indicate that there is much variation in the cross-sectional size and shape of columns. Some columns are more or less round or polygonal, and for these one can speak in rough terms of a cross-sectional diameter. Others seem to be long



Text-fig. 3. Map showing receptive-field orientations of cells encountered near the surface, in 31 cortical penetrations. Region situated near anterior end of post-lateral gyrus. Interrupted lines separate regions of relatively constant receptive-field axis orientation, and partially outline 3 columns. Scale, 1 mm. (See also Pl. 1.)

and narrow, like the one defined by penetrations 18–24 in Text-fig. 3. We have no way of estimating the upper or lower limits of the cross-sectional size of cortical columns, but some of them must be less than 100μ across, while the long narrow ones may extend for at least 2 mm or more along the cortical surface. At the surface of the apical segment of the post-lateral gyrus an average diameter (where this term applies) might be about 0.5 mm, an estimate which agrees with previous ones based on deep micro-electrode penetrations (Hubel & Wiesel, 1962). At present we do not know

if columns vary in size in different parts of the striate cortex, for example in regions receiving projections from peripheral, as opposed to central, parts of the retina.

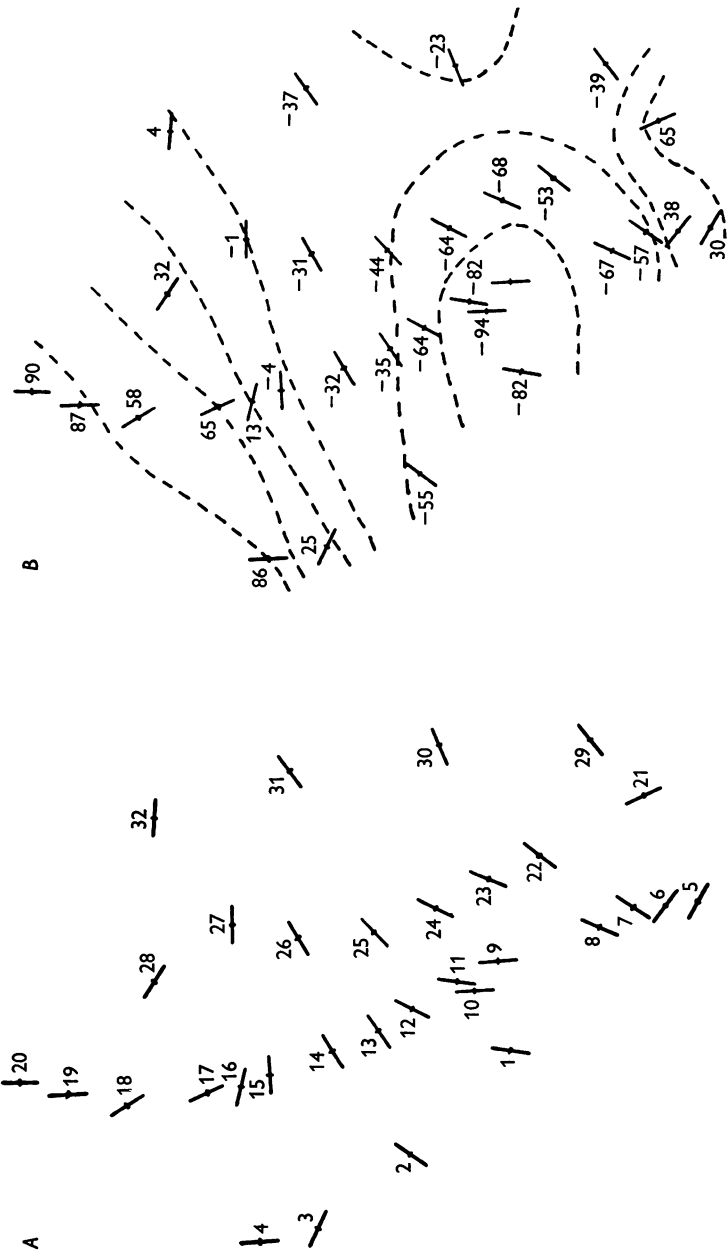
Arrangement of columns

There have been indications, both from single deep penetrations and from surface maps, of some order in the arrangement of neighbouring columns. An example is seen in penetration 2 of Text-fig. 1. Here the four shifts in orientation were small, ranging from 22 to 31° and averaging 25°, and all shifts were in the same direction. Small-step sequences such as this were not rare in penetrations through the cortex, but they were by no means the rule; shifts in orientation of 60–90° were seen a few times in most penetrations, and in some experiments (e.g. Text-fig. 13 and 14, Hubel & Wiesel, 1962) there was no hint of any order in the sequences of receptive-field orientations. Yet ordered sequences were just common enough, and impressive enough when they occurred, to make one feel that they were not entirely fortuitous.

Hints of systematic placing of columns were present in all surface maps made from multiple superficial penetrations. For example, in Text-fig. 3 some order may be seen in the sequence formed by penetrations 10, 17, 20–24 and 25 and also in penetrations 15, 10, 11 and 12. In two experiments this orderliness was so pronounced that there could be little question of its being a chance occurrence.

The best example of a systematic arrangement of columns is shown in Text-fig. 4 and Pl. 2. Here 32 points were mapped over an area $2 \times 1\frac{1}{4}$ mm. The penetrations are numbered in Text-fig. 4A and the corresponding receptive-field angles are indicated in Text-fig. 4B (0° corresponds to a horizontal orientation). In the sequence formed by penetrations 7–20 neighbouring points either showed about the same orientation (to within $\pm 5^\circ$) or else differed by an amount averaging 25°. Except for a shift of 52° between penetrations 16 and 17, all differences were less than 30°. Besides being small the changes in orientation in successive penetrations tended to be in the same direction, counter-clockwise in penetrations 7–10 and clockwise in penetrations 10–20. An equally well ordered sequence was found in penetrations 22–28, and here the changes in orientation in successive penetrations tended to parallel those of the sequence 7–20. The map as a whole, especially in its posterior portions, suggested an ordered series of long narrow columns oriented for the most part medio-laterally. As indicated in Text-fig. 4B by the interrupted lines, the entire map can be interpreted in a manner consistent with the assumption that this region of cortex is arranged in an orderly way.

Within the regions mapped in Text-figs. 3 and 4, which receive projections from the retinal area centralis, there were no perceptible systematic



Text-fig. 4. Surface map of a region in post-lateral gyrus. Receptive-field orientations are shown for 32 superficial penetrations. In *A* penetrations are numbered in sequence. In *B* receptive-field orientations are given in degrees of arc, zero corresponding to a horizontal orientation. Interrupted lines are drawn to separate regions of relatively constant axis orientation. Scale, 1 mm. (See also Pl. 2.)

differences in receptive-field positions; the average field position showed no obvious change from one column to the next, or from one end to the other of a single column. This is consistent with previous results (Hubel & Wiesel, 1962, p. 134). In this part of the cortex any changes in position that occur with a movement of 2–3 mm across the cortex are apparently not detectable, probably because they are small compared with the random staggering in receptive-field positions from one cell to the next.

DISCUSSION

The experiments reported here confirm and extend our previous impression that cells in the striate cortex are segregated into regions according to their receptive-field orientation. Like similar subdivisions described for the somato-sensory cortex by Mountcastle (1957) and Powell & Mountcastle (1959), the regions are columnar in shape and appear to extend from surface to white matter. Moreover, recordings and lesions made during multiple deep micro-electrode penetrations through the cortex make it clear that the columns are radially arranged, with their walls parallel to the bundles of myelinated fibres and perpendicular to the cortical layers. Maps made by superficial penetrations show that the columns are variable in size and often irregular in cross-sectional shape. Some appear to be oval or polygonal in cross-section, but others are elongated, and may extend across part of a gyrus and yet be only a few tenths of a millimetre in width.

Hints of ordered sequences of columns, seen in portions of surface maps and in occasional deep penetrations, were originally thought to be chance occurrences. Some maps showed almost no regularity, and in deep micro-electrode penetrations shifts in orientation of 45–90° were fairly frequent. Nevertheless, maps such as that of Text-fig. 4 make it clear that the columns are arranged in a systematic way in at least some parts of the striate cortex. We have recently found overwhelming evidence that this is the case in parts of the monkey striate cortex (Hubel & Wiesel, unpublished). Thus it would seem that there are regions of cortex that are ordered, and regions that are not.

A map such as that of Text-fig. 4 may seem to suggest that receptive-field orientation varies in a continuous manner rather than in discrete steps as the surface of the cortex is traversed. While strictly continuous gradations are in a sense not possible, since the cortex consists of discrete units, the nerve cells, it still may be asked whether in these regions receptive-field orientations do not change in steps too small to measure as one proceeds along the cortex. The best evidence that this is not so is seen in deep cortical penetrations showing regular shifts, as in Text-fig. 1, penetration 2. Here the unresolved background activity gave a continuous

record of the receptive-field orientation, and indicated that the columns were discrete and considerably more than one cell wide.

Finally, it may be asked whether the tendency to ordered arrangements of columns has any functional significance. It seems reasonable to suppose that the closer cells are in a nervous structure the better their chances will be of having interconnexions or of sharing connexions: there is at least a certain economy in having cells that share connexions close to one another. Within one column the projections of lateral geniculate cells upon simple cortical cells presumably involve certain groupings of the afferent fibres. For example, axons of geniculate cells whose field centres lie along lines parallel to the common receptive-field axis of the column may be grouped together (Hubel & Wiesel, 1962, Text-fig. 19). A given system of fibre groups would be appropriate only to cells with a particular receptive-field orientation; for cells in a different column, with another receptive-field orientation, the groups would not be appropriate without modification. A new group, appropriate to a new orientation, might be formed from an old one by dropping some geniculate fibres and replacing them with others. Fibres common to the two groups would then supply both columns. In an area of cortex in which adjacent columns had orientations that were not too far apart (as in Text-fig. 4) groups of geniculate-fibre terminals might run for some distance, crossing several columns. Some of the fibres making up a bundle would change at each column boundary, but a complete rearrangement would not be necessary. There would thus be a considerable advantage for columns with almost the same field orientations to be close to one another.

In conclusion we may emphasize that the columns described here are defined in functional rather than anatomical terms. Except for the deep radial fibre bundles which parallel the columnar walls, the columns have no known anatomical correlates. Yet, as suggested in the last paragraph, the functional properties of cortical neurones must depend on anatomical connexions, and these must differ in some consistent way from one column to the next. To determine the morphological differences between two neighbouring columns thus represents a challenging neuro-anatomical problem and one of great interest from a functional point of view.

SUMMARY

1. Previous studies have shown that the striate cortex of the cat is subdivided into columnar regions of cells having a common receptive-field axis orientation. The present paper describes further observations on the shape and arrangement of the columns.

2. From multiple parallel penetrations the walls of columns appear to

be parallel to the radial fibre bundles of the cortex and perpendicular to the cortical layers.

3. The surface mosaic formed by the intersection of the columnar walls with the cortical surface is highly irregular. Some columns appear to be 'compact' in shape (more or less round or oval), while others seem to be very long and narrow.

4. In some parts of the cortex columns are arranged in a very regular manner. Here the discrete shifts in orientation as one moves along the cortical surface in a straight line are small, and the direction of the shifts may be the same, clockwise or counterclockwise, over long sequences. In these ordered regions the columns are especially likely to be long and narrow. In other parts of the cortex there appears to be little if any order to the arrangement of neighbouring columns.

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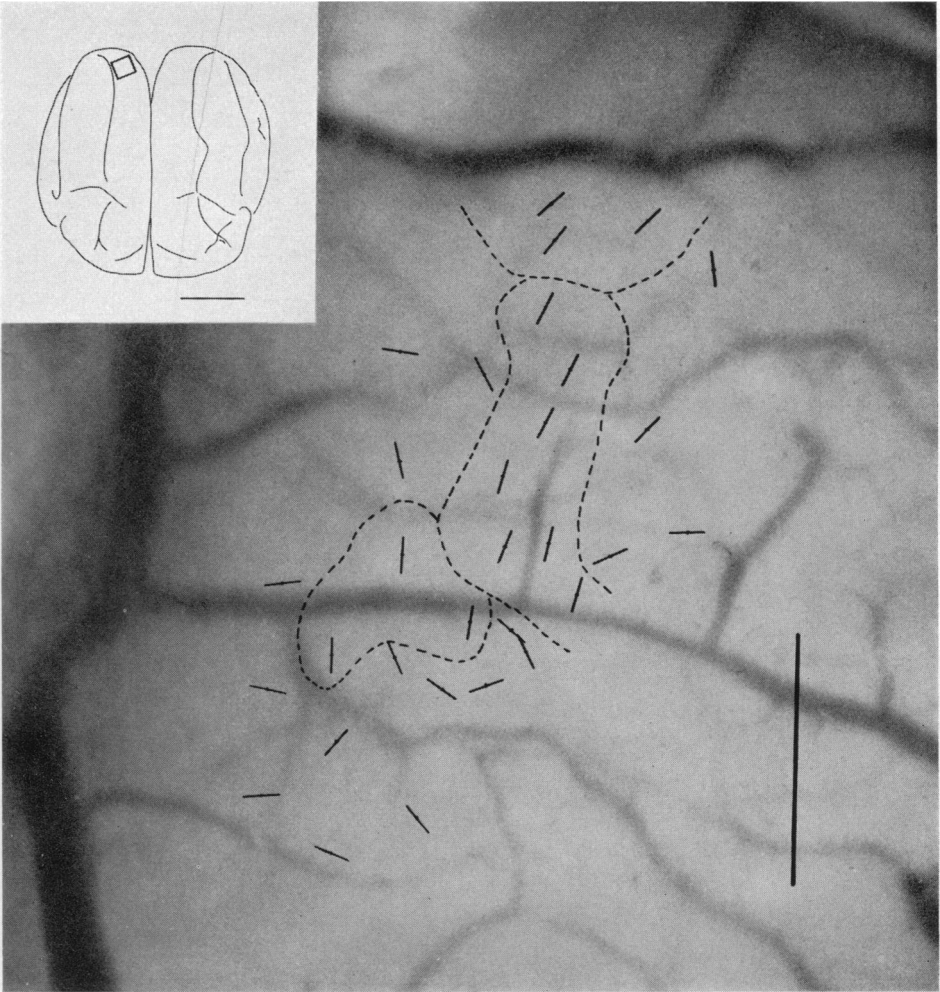
EXPLANATION OF PLATES

PLATE 1

Photograph of cortical surface showing region mapped in Text-fig. 3; scale, 1 mm. Inset shows area of brain photographed; scale of inset, 1 cm.

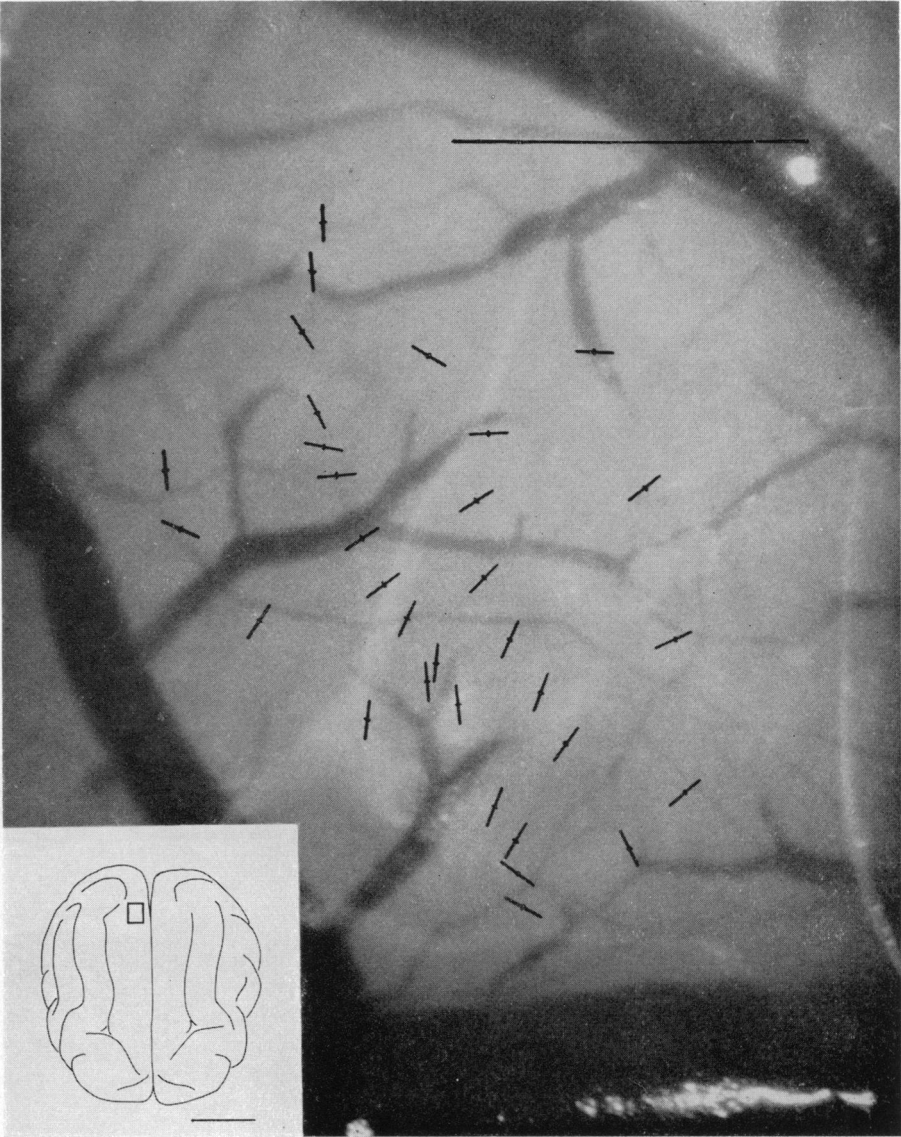
PLATE 2

Photograph of cortical surface showing region mapped in Text-fig. 4; scale 1 mm. Inset shows area of brain photographed; scale of inset, 1 cm.



D. H. HUBEL AND T. N. WIESEL

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D. H. HUBEL AND T. N. WIESEL