

Short Communications

Projection into the visual field of ocular dominance columns in macaque monkey

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(Accepted November 18th, 1976)

Since the first reports of aggregations by ocular dominance of cells in monkey striate cortex^{2,3}, the geometry of these groupings has become increasingly clear. The columns have been reconstructed anatomically, first using the Wiitanen modification of the Nauta-Fink-Heimer method^{1,9}, then by autoradiography following eye injection of labeled material⁸, and finally by a reduced silver method staining tangentially running fibers in layer IV C⁷. All of these methods show that the aggregations as seen in a face-on, surface view are actually parallel stripes with varying numbers of cross-linkages, bifurcations and blind endings.

Fig. 1A gives an example of such a reconstruction made from serial sections stained by the reduced silver method (adapted from ref. 7, Fig. 8a); it shows the entire exposed surface of a macaque monkey's right occipital lobe, representing a region of visual field that extends from the fovea out to about 9°. In Fig. 1A alternate stripes have been inked in to show the two-fold nature of the subdivisions; the dark stripes can be imagined to represent the projections of the left eye onto layer IV C and the light stripes the projections of the right eye, or the reverse: in this animal we made no recordings and hence do not know which set corresponded to the left eye and which to the right. The continuation of the stripes into the calcarine fissure is shown in Fig. 1B and C; here again alternate stripes are inked in, and again the choice of which set to show as dark is arbitrary. These fragments extend the reconstruction out to about 25°. A narrow gap between the three pieces, about 1 mm wide, occurs at the folds where the cortex was sectioned at an angle that was too far from tangential to allow the fiber bands to be seen.

Our object in the present study was to learn roughly how the cortical stripes would appear if transposed into the visual field. Certain predictions can be made from what is already known. A conspicuous feature of the anatomical stripes is the constancy of their width, about 400 μm , from the fovea out almost as far as the monocular crescent⁸. The representation of the visual fields on the cortex is far from uniform, however: it is detailed in the foveal region and becomes coarser with eccentricity. As transformed

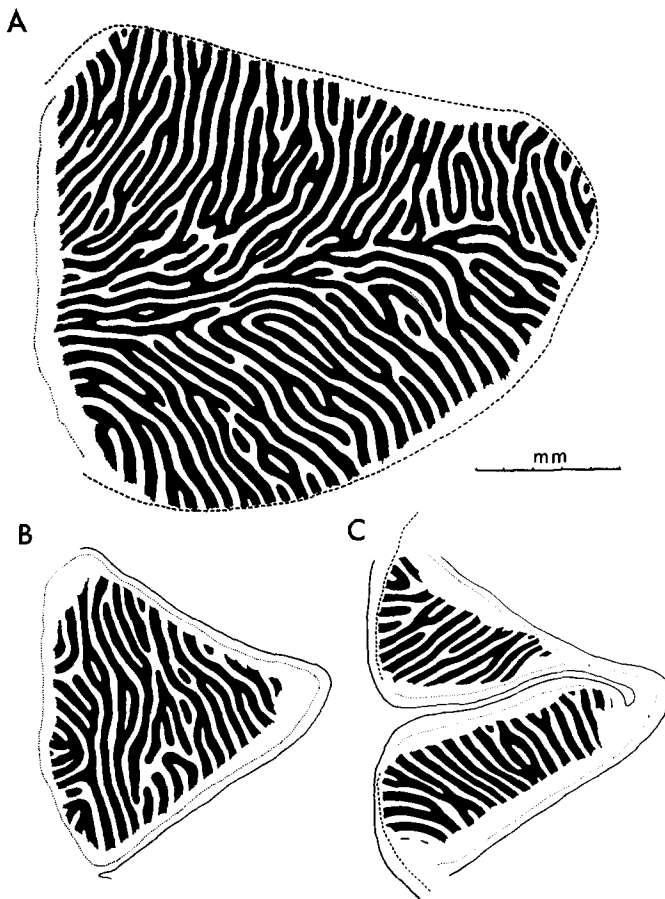


Fig. 1. Reconstruction of ocular dominance columns from a macaque monkey right occipital lobe, prepared from a set of serial sections roughly tangential to the exposed surface of the occipital lobe, and stained by the reduced silver method of Liesegang⁷. In the diagram every other column has been inked in; thus the dark stripes in the figure correspond to one eye and the light stripes to the other. A: stripes on the exposed surface of the occipital lobe. Lateral is to the right; anterior is up. The dashed \cup -shaped line represents the 17–18 border (vertical meridian); at the extreme right, where this line curves around sharply, is the foveal representation. The dotted line at the medial edge (left, in the figure) indicates where the cortex bends over abruptly to continue as a buried fold. The region of cortex shown represents visual field from fovea out to about 9° . B: the continuation of A as a buried fold, one level deeper. This is in reality positioned below A, with the medial parts of the dotted lines superimposed. The more lateral, \cup -shaped part of this dotted line suggests the position of another pair of folds, where the cortex continues into a third, still deeper pair of shelves. These are shown in C. B and C together continue the visual-field representation, from 9° out to about 25° .

into the visual fields the projections must therefore vary in width with distance from the center of gaze, being narrow near the center and becoming progressively wider as eccentricity increases. We wished not only to visualize this increasing coarseness of representation, but also to learn more about the pattern of the stripes in relation to the field of vision.

In a previous study⁵, magnification (mm of cortex per degree of visual field) was determined at several eccentricities, ranging from 1° to 22° . Fig. 2 shows a graph of

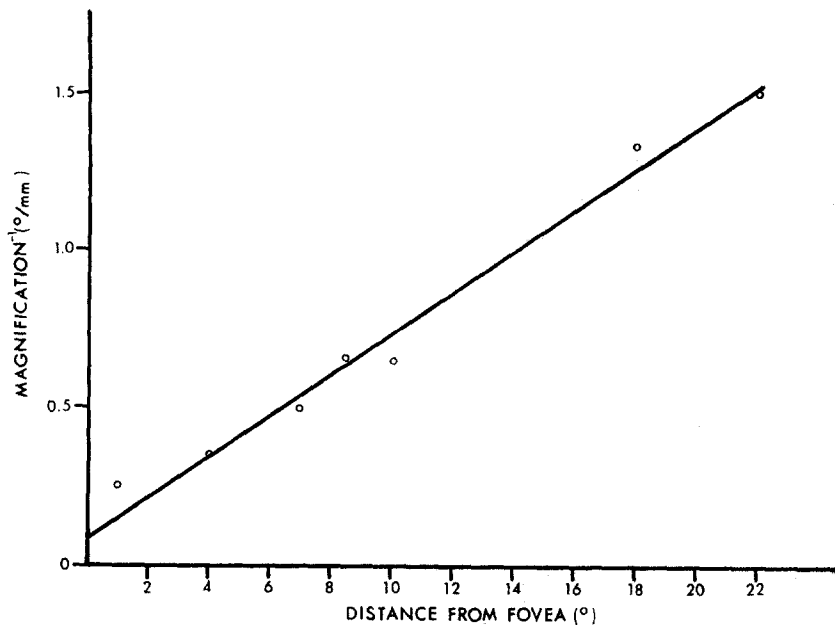


Fig. 2. Graph of reciprocal magnification vs. distance from fovea, in the visual field, for macaque striate cortex. Reciprocal magnification is the number of degrees of visual field corresponding to 1 mm on the cortex. This varies with position on the cortex, i.e., with position in the visual field, increasing roughly linearly with visual-field distance from the fovea (also called eccentricity or E). The line is the regression line for 7 values of M^{-1} determined at 7 different eccentricities⁵; it has a slope of 0.0637 mm^{-1} and an intercept of 0.109 .

reciprocal magnification (M^{-1}) plotted against eccentricity E . In agreement with Daniel and Whitteridge¹, the relationship is roughly linear, and Fig. 2 shows the regression line for the 7 points. The available evidence from our work⁵ and that of Daniel and Whitteridge¹ suggests that M is a function of E only, and is not, for example, very different for the representation of the field of vision in the superior and inferior quadrants or along the horizontal meridian as opposed to the vertical. If that is so, it should be possible to determine the visual-field coordinates of any point on the cortical surface within the 22° limit. Transposing the stripes can then be done point-by-point, a task that would be tedious by hand but is easily done with the help of a computer.

The equation for the regression line of Fig. 2 is:

$$M^{-1} = \frac{dE}{dx} = 0.0637E + 0.109 \quad (1)$$

where E = eccentricity, in degrees, and x = distance of the cortical point from the foveal representation, in mm.

Taking reciprocals of both sides and integrating from 0 to x , we have

$$x = 15.70 \log_e (0.584E + 1) \quad (2)$$

or

$$E = \frac{e^{0.0637x} - 1}{0.584} \quad (3)$$

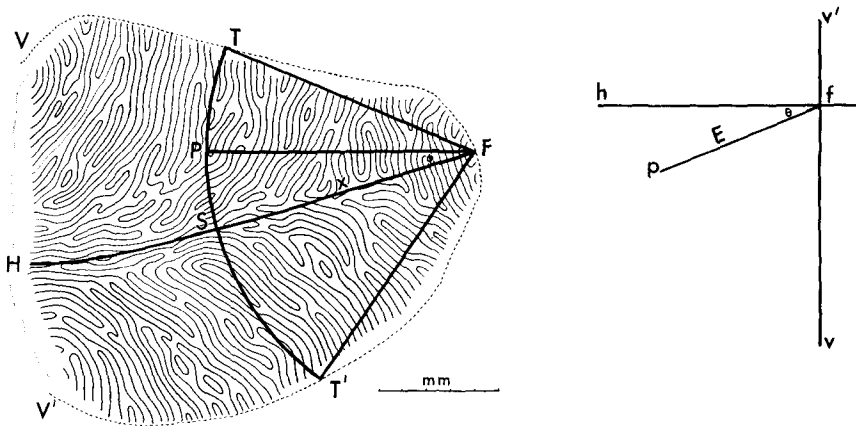


Fig. 3. Diagram to illustrate the procedure for calculating the visual-field coordinates of any point P on the striate cortex. In the left-hand diagram, F is the foveal representation on the cortex, the dashed line VFV' is the 17-18 border, representing the vertical midline, HF is the horizontal meridian drawn by eye along the path of confluence of the stripes as they stream in from VF and V'F. TT' is the arc of a circle drawn on the diagram, whose center is F and which passes through P, intersecting FH at S. $FS = x$ and $\angle PFH = \Phi$, so that (x, Φ) are the coordinates of P. The right-hand diagram represents the visual field. We let $p(E, \theta)$ correspond to P on the cortex: because of the way the macaque cortex is laid out p will be in the inferior visual field since P is anterior to the horizontal meridian representation FH. vv' in the right-hand diagram is the vertical midline passing through the foveal projection f; fh is the horizon. The problem is to express E and θ in terms of x and Φ .

Let P be any point on the cortex (Fig. 3), and suppose F is the representation of the fovea. The representation of the vertical meridian (the 17-18 border) is the dashed line VFV'. Let FH be the presumed horizontal meridian representation, drawn by eye along the path of convergence of the two sets of columns as they stream in from the 17-18 border. (That the horizontal meridian is represented at this line of confluence is known from physiological recordings from brains in which columns were later visualized anatomically.) We draw the arc of a circle with center F through P, intersecting FH at S, and FV and FV' at T and T'.

Suppose the coordinates of P are (x, Φ) where

$$x = FP = FS$$

$$\Phi = \angle PFH$$

Let the corresponding point p in the visual field be represented by (E, θ) , where E = eccentricity in degrees, already known in terms of x from equation (3), and $\theta = \angle pfh$, where f is the foveal projection in the visual field and fh is the horizontal meridian.

For any point P (x, Φ) the angles TFS and T'FS will be functions of x. These angles in the diagram were measured for 10 equally spaced points along FSH (i.e., for 10 values of x), and other values could then be estimated by interpolation.

$$\text{Then we assume: } \frac{\theta}{90^\circ} = \frac{\Phi}{\angle TFS}$$

θ

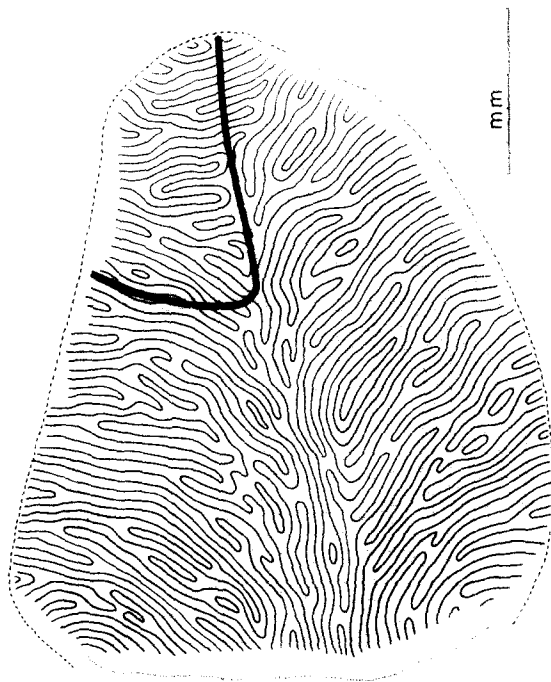
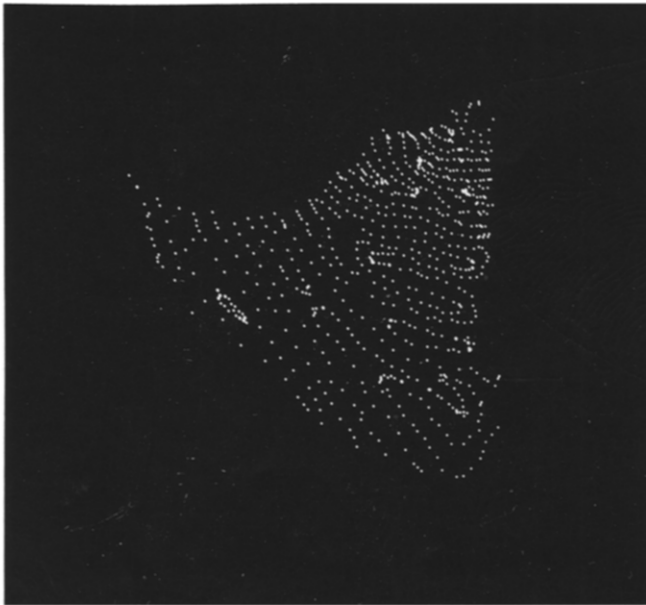


Fig. 4. The projection for one segment of the cortex. Left-hand diagram shows the piece of cortex to be represented, outlined by the heavy curve. The stylus of the X-Y tablet is made to skip along the lines that form the column borders, making contact roughly every 0.25 mm. The resulting computer display is shown on the right. In the cortex, the fovea is represented at the extreme right; in the display it is represented in the lower right corner. To make a comparison easier, the dot representation is shown



Fig. 5. Visual-field reconstruction of roughly the inner 9° , corresponding to A in Fig. 1. Since the part reconstructed is from the right hemisphere, the projection is into the left visual field. Anterior areas, in front of the horizontal meridian representation (above FH, in Fig. 3), project to the inferior visual field, areas behind the meridian project to the superior field.

(For negative values of θ we change the sign and substitute $\angle T'FS$ for $\angle TFS$.)

Thus for any point P, p can be determined in terms of x and Φ .

This procedure was carried out for points roughly 0.25 mm apart on all the column boundaries by tracing along the lines with a stylus on a graphic X-Y data tablet, computing the transformation with a PDP-12, and displaying the results. Because of the limitations of this computer the transformation had to be broken up into 6 segments which were photographed and later spliced together. Fig. 4 shows a sample representation of the area indicated by the heavy line in the cortical map.

The transformation of stripes in the central 9° (Fig. 1A) is shown in Fig. 5. By adopting a similar procedure for the additional 3 calcarine cortical segments and assuming a gap between the segments about 1 mm in width, the extended reconstruction out to 25° was obtained, as shown in Fig. 6.

Figs. 5 and 6 provide some visual indications of the rate of increase in the coarseness of the visual field representation of columns, with increasing eccentricity. In agreement with a previous suggestion⁷, Fig. 6 indicates that the columns, as projected into the visual fields, have roughly a concentric arrangement about the fovea. Between 1° and 9° there is an apparently competing tendency for the stripes near the horizontal meridian to be horizontally arranged.



Fig. 6. Complete reconstruction out to about 25° , including parts B and C of Fig. 1.

The arrangement shown in Figs. 5 and 6 is only a very rough approximation. Fig. 1A represents a convex structure projected onto a plane surface, which produces a moderate foreshortening of the column boundaries close to the 17–18 border; Figs. 5 and 6 involve mapping part of a spherical surface on a plane — and so on. An accurate mapping, while possible in principle, would call for far more computer capacity than was at our disposal.

Equations 1–3 allow one to make several predictions. If we assume that the binocular visual field extends temporally from the midvertical in the monkey for 75° , the corresponding cortical distance would, from equation 2, be about 60 mm. If the columns are $400 \mu\text{m}$ in width, this would suggest a total of about 150 stripes in each hemisphere. The actual extent of the binocular fields in the monkey is not known, but errors in the figures make little difference to the number of columns: if the binocular overlap extended to 90° the number of stripes would be 156; if they were limited to 60° , it would be 140. Stripe widths, projected into the visual fields, should be 0.04° at the fovea, 0.27° at 9° eccentricity, 0.67° at 25° and about 2° at 75° .

Equation 3 allows us to predict the size of the cortical representation of the optic disc and roughly its position. The disc is centered approximately on the horizontal meridian 16° in the temporal visual field, with a diameter of about 6° . The distance

along the cortex from fovea to disc center should therefore be 36.7 mm and the diameter of the cortical representation along the horizon representation comes to about 5.4 mm. This could place the disc representation somewhere in the roof of the buried calcarine fold, about 6 mm lateral to the midline. It should thus show in Fig. 1B: why it does not is not clear, but it may be that it was closer than usual to the mesial surface of the cortex in this particular monkey and hence was not sectioned tangentially. If our calculations are correct, the disc should occupy a width of cortex equal to 13.5 stripes (or about 7 pairs of stripes).

The reconstructions of Figs. 5 and 6, it should be emphasized, are in a sense merely formal representations; were they to be taken literally one might gain the impression that half the visual world (the dark stripes) is seen by one eye and the other half (the light stripes) by the other. In fact each set of stripes in layer 4 sees the entire visual world. This is accomplished by compressing by a factor of 2 the visual field representation in layer IV C, in a direction at right angles to the stripes. At the stripe borders the representation is discontinuous, so that in crossing a border the transition from one eye to the other is accompanied by a jump in the corresponding position in the visual field, equal to half the width of one projected stripe. A preliminary account of this layer-IV anisotropy has already appeared⁶ and is to be published in more detail.

We wish to thank Carolyn Scott for photographic assistance.

Supported by National Institutes of Health Grant EY00605 and The Rowland Foundation, Inc.

- 1 Daniel, P. M. and Whitteridge, D., The representation of the visual field on the cerebral cortex in monkeys, *J. Physiol. (Lond.)*, 159 (1961) 203–221.
- 2 Hubel, D. H. and Wiesel, T. N., Binocular interaction in striate cortex of kittens reared with artificial squint, *J. Neurophysiol.*, 28 (1965) 1041–1059.
- 3 Hubel, D. H. and Wiesel, T. N., Receptive fields and functional architecture of monkey striate cortex, *J. Physiol. (Lond.)*, 195 (1968) 215–243.
- 4 Hubel, D. H. and Wiesel, T. N., Laminar and columnar distribution of geniculo-cortical fibers in the macaque monkey, *J. comp. Neurol.*, 146 (1972) 421–450.
- 5 Hubel, D. H. and Wiesel, T. N., Uniformity of monkey striate cortex: a parallel relationship between field size, scatter, and magnification factor, *J. comp. Neurol.*, 158 (1974) 295–306.
- 6 Hubel, D. H., Wiesel, T. N. and LeVay, S., Visual-field representation in layer IV C of monkey striate cortex, *Fourth Annual Meeting, Society for Neuroscience, St. Louis, Mo., October 20–24, 1974* (abstract).
- 7 LeVay, S., Hubel, D. H. and Wiesel, T. N., The pattern of ocular dominance columns in macaque visual cortex revealed by a reduced silver stain, *J. comp. Neurol.*, 159 (1975) 559–576.
- 8 Wiesel, T. N., Hubel, D. H. and Lam, D. M. K., Autoradiographic demonstration of ocular-dominance columns in the monkey striate cortex by means of transneuronal transport, *Brain Research*, 79 (1974) 273–279.
- 9 Wiitanen, J. T., Selective silver impregnation of degenerating axons and axon terminals in the central nervous system of the monkey (*Macaca mulatta*), *Brain Research*, 14 (1969) 546–548.