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"Geometry of Orientation Columns in the Visual Cortex"

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Geometry of Orientation Columns in the Visual Cortex

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Abstract. The optimal direction of lines in the visual field to which neurons in the visual cortex respond changes in a regular way when the recording electrode progresses tangentially through the cortex (Hubel and Wiesel, 1962). It is possible to reconstruct the field of orientations from long, sometimes multiple parallel penetrations (Hubel and Wiesel, 1974; Albus, 1975) by assuming that the orientations are arranged radially around centers. A method is developed which makes it possible to define uniquely the position of the centers in the vicinity of the electrode track. They turn out to be spaced at distances of about 0.5 mm and may be tentatively identified with the positions of the giant cells of Meynert.

The appropriate stimulus for most neurons in the visual cortex of anesthesized cats and monkeys is not diffuse light, nor a spot of light surrounded by darkness or a dark spot on a light background, but a line with a certain orientation in the visual field. This discovery (Hubel and Wiesel, 1959) was followed by many more (summarized in Hubel and Wiesel, 1977; Bishop et al., 1971; Schiller et al., 1976) which provide a good picture of the line detectors in the cortex, or movement detectors, as they may also be called, for the effect on the cortical cell is usually more pronounced when the line is moved, at right angle to its extension, in one or the other or in either direction. At the present stage it is not possible, however, to explain the line or movement detectors on the basis of the shapes and connections of the neurons in the visual cortex, although it is known that the apparatus responsible for the detection must be housed in a region of cortex with a diameter of approximately 1 mm.

The distribution of movement detectors within the tissue of the visual area follows two remarkable rules (Hubel and Wiesel, 1962): first, neurons with cell bodies aligned in a vertical direction within one narrow column of cortex tend to respond optimally to lines with one and the same orientation. Second, neurons in different columns generally respond to different orientations, so arranged that continuous movement through the cortex corresponds, barring singularities, to a continuous rotation of the corresponding orientation. It is to this layout of line detectors in the cortical plane that we want to turn our attention here.

For our purpose, the following facts are important.

1) In the monkey (Hubel and Wiesel, 1974a) the change of orientation specificity with the movement of the recording electrode through the cortex is very "regular". When the orientations are plotted as a function of distance, the results can be fitted by smooth curves, with little scatter of the individual orientations. By comparison (Hubel and Wiesel, 1974b) mapping of points in visual space on the visual cortex seems much more erratic. The situation is similar in the cat (Albus, 1975a, b), although there the scatter of orientations may be somewhat larger.

2) The change of orientation per cortical distance typically is between 100°/mm and 200°/mm both in the cat and the monkey. It may occasionally exceed 300°/mm, and there are stretches where the orientation stays constant for a few hundred microns.

3) In about half of the penetrations (Hubel and Wiesel, 1974a) the change of the orientation with the movement of the electrode is clockwise for part of the trajectiory, counterclockwise for another part. There may be several transitions from one sense of rotation to the other in one penetration.

4) Occasionally there is an abrupt change in an otherwise smooth progression of the orientations along a straight line in the cortex (Hubel and Wiesel, 1974a; Albus, 1975b).

From the evidence provided in the published records, one should like to reconstruct the distribution of

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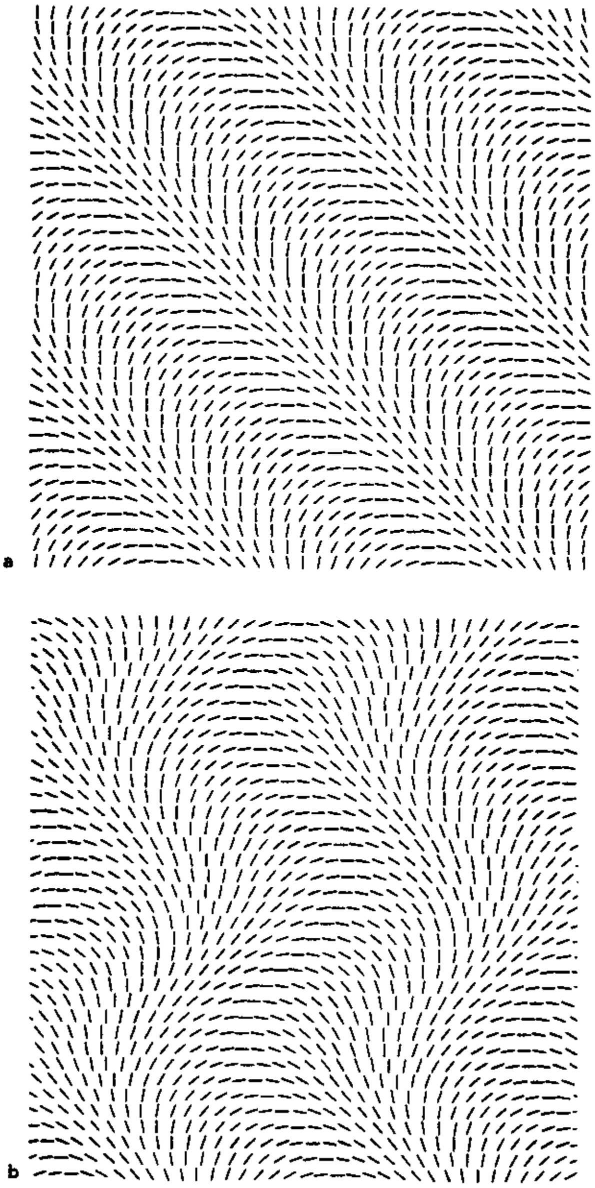

Fig. 1a and b. Fields of orientation with straight a and wavering b iso-orientation lines

orientations over the cortical surface. The simple distribution of Fig. 1a, with a continuous rotation of the orientations in one direction (lower left to upper right in the illustration) and lines of equal orientation at right angles to this, is not compatible with the changes from counterclockwise to clockwise rotation of the orientation along a straight path, nor with the abrupt changes of orientation which are sometimes encountered. Figure 1b, with wavering lines of equal orientation, explains the changes from clockwise to counterclockwise (along vertical lines in the figure) but does not account for the jumps. These could be due to occasional bifurcations of the lines of equal orientations, as might easily occur for reasons connected with the intrinsic geometry of bent surfaces, such as that of the visual cortex, and as have been actually observed in that other pattern of stripes formed by the ocular dominance "columns" or "slabs" (Hubel and Wiesel, 1972). However, we believe that the most natural explanation of the facts observed would be in terms of orientations arranged with circular symmetry around centers, either radially (Fig. 2a) or along concentric circles (Fig. 2b). We will show that the records published by Hubel and Wiesel (1974a) and by Albus (1975b) can be fitted rather neatly by curves derived from such a centric model.

For simplicity of exposition, we shall confine our argument to the case of Fig. 2a, which is equivalent, except for a rotation of 90° to that of Fig. 2b. Suppose the neurons in the visual cortex respond to orientations given by the lines in the diagram. An electrode passing by a center would then record from neurons with continuously rotating orientation, except when it leaves the region of one center to enter the next (Fig. 2a, arrows). If within one region the electrode has the center to its left, the rotation will be counterclockwise. Depending on the angle of the penetration, in the next region it may again have the center to its left, or to its right, in which case there would be a change from counterclockwise to clockwise (Fig. 2a, lower arrow). It is easy to convince oneself that going from clockwise to counterclockwise there may or may not be a discontinuity, a jump in the orientation (lower arrow), while in passing from one clockwise (counterclockwise) region to the next there must be a jump (Fig. 2a, upper arrow). Occasionally, if the electrode penetrates exactly along the path between two centers, there may be no change of orientation. Otherwise, the closer the track is to the center, the faster the rotation per unit distance travelled. Thus it is clear that within each region belonging to one center the rotation of the orientation will be slow at first, then faster and then again slower.

These intuitively obvious properties of the centric array of orientations lead to the following rules (Fig. 3): 1) A plot of orientation (in degrees) vs. distance must consist of sigmoid pieces, spanning no more than the distance between two neighbouring centers along the abscissa (representing the electrode path) and no more than 180° on the ordinate (representing the orientations). These sigmoid pieces may be ascending (Fig. 3b, representing clockwise rotation) or descending (Fig. 3a, counterclockwise rotation). 2) Two consecutive ascending (descending) sigmoid pieces must be separated by a jump in the plot (Fig. 3b). 3) All the ascending and descending sigmoid pieces of one plot must have their points of maximum (ascending or descending) steepness at a level of the ordinate corresponding to one and the same orientation, namely the

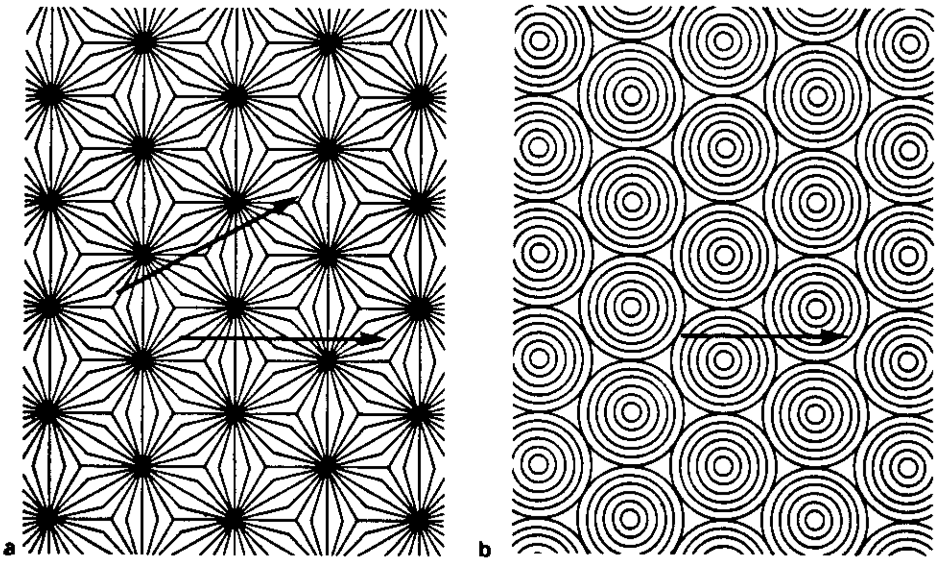

Fig. 2a and b. Centric arrays of orientations. **a** radial, **b** concentric. Arrows: movement of an electrode through the array produces certain regular changes of orientation

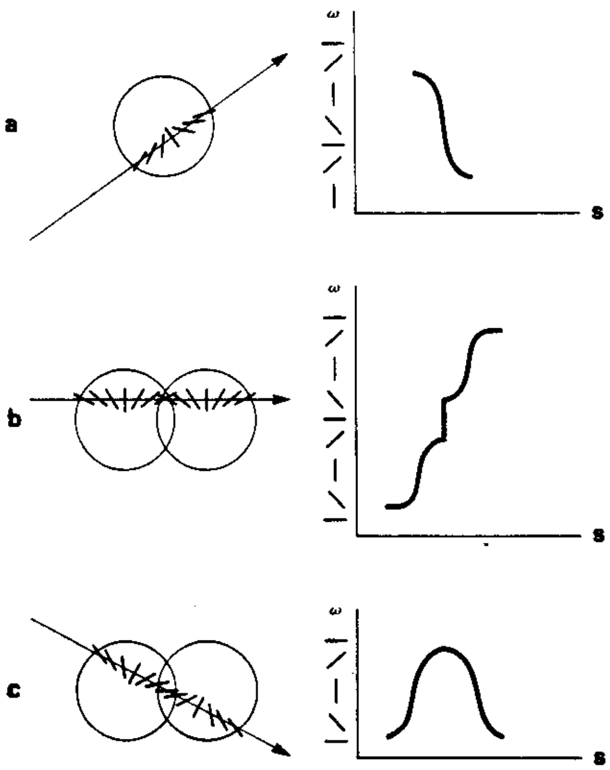

Fig. 3a–c. Various pieces of curves that are to be expected with penetrations of a centric array of orientations. ω: orientation, s: distance

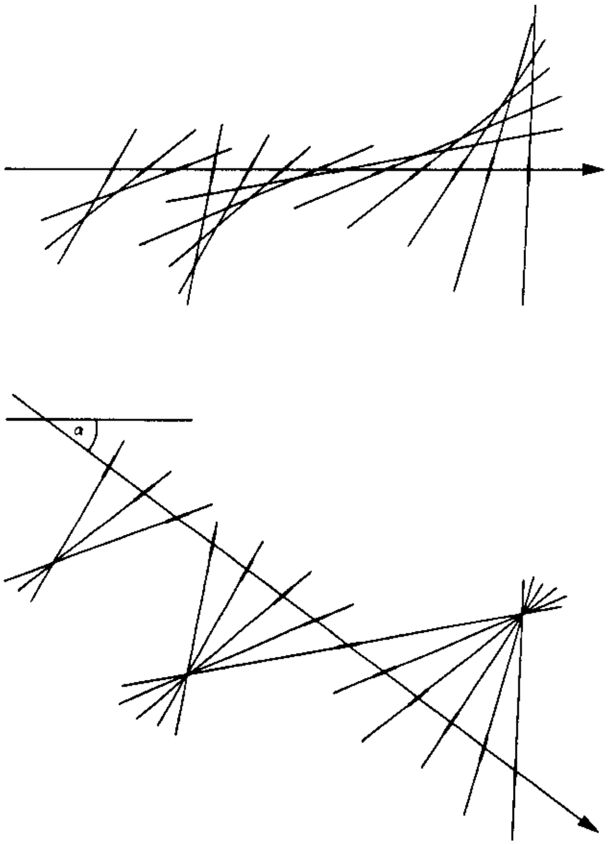

Fig. 4. Sets of orientations encountered along an electrode track will not meet in common centers (upper diagram) unless the direction of the electrode is drawn correctly in the coordinate system in which the orientations are given (lower diagram)

orientation at right angles to the electrode path (Fig. 3b, c). 4) Where there are jumps in the plot, these must cross levels of the ordinate separated by 90° from the level of maximum steepness (Fig. 3b), i.e. the level corresponding to the orientation of the electrode track.

To test the fit of the model with the plots published by Hubel and Wiesel (1974a) and by Albus (1975b) we proceeded as follows.

First, the plots were fitted by hand with curves consisting of sigmoid pieces and jumps, according to

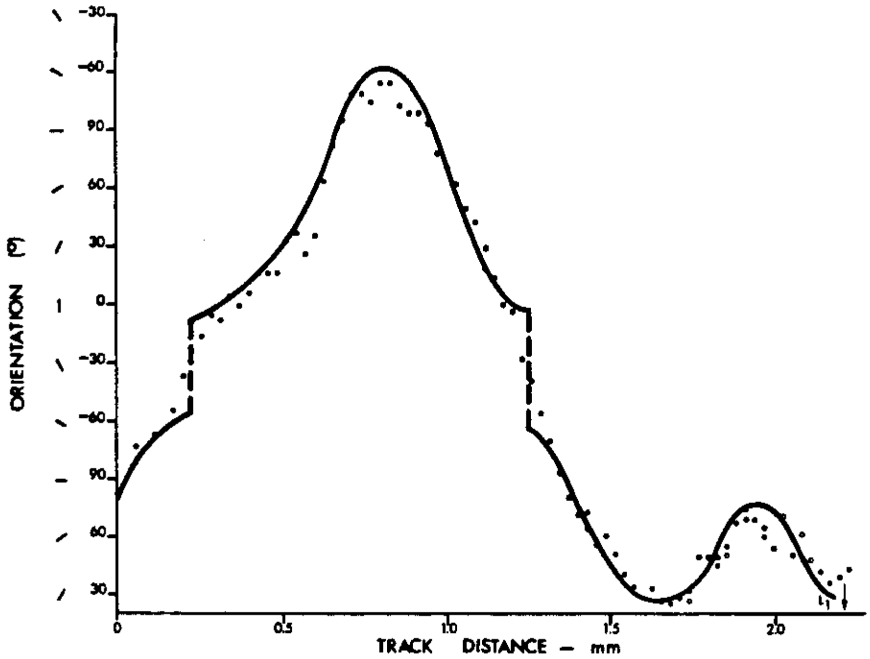

Fig. 5. Modified from Hubel and Wiesel (1974a). The curve is obtained from the hypothetical map of the centers in Fig. 6

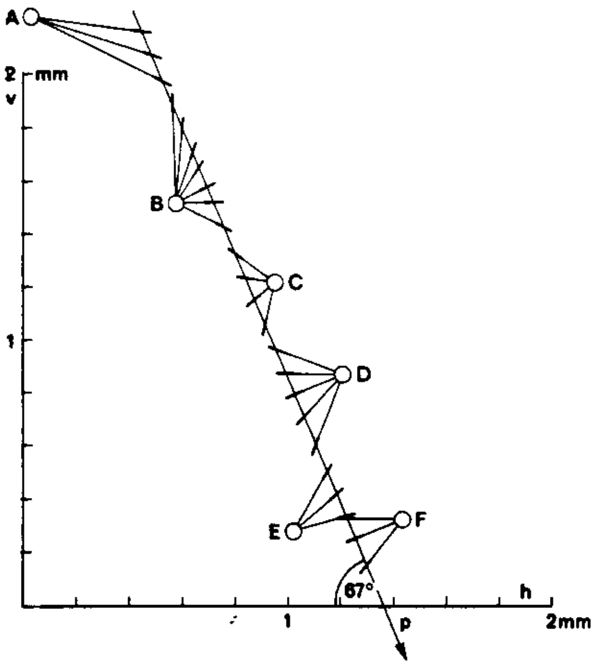

Fig. 6. Map of the centers corresponding to the plot of Fig. 5. *A – F*: centers. Arrow: electrode track

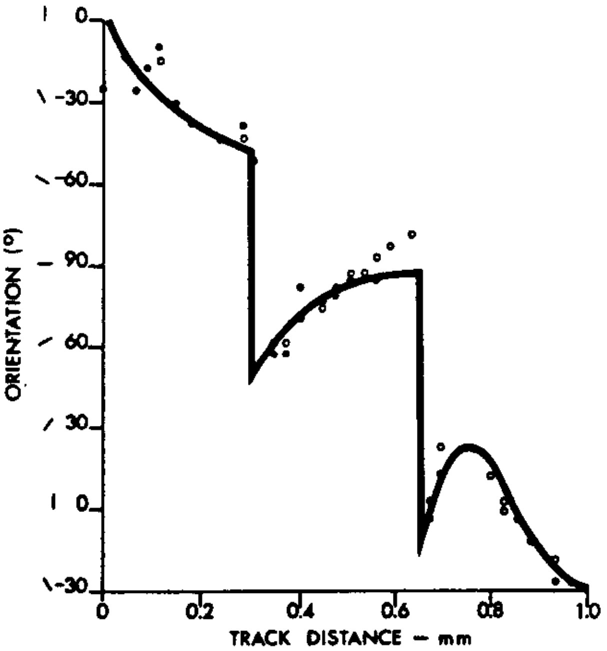

Fig. 7. From Hubel and Wiesel (1974a). The curve is derived from the reconstruction of the centers in Fig. 8

the above rules. Sometimes several fits were possible, in that it was possible to give the steep stretches of the curve the alternative interpretation of jump or maximum slope, but in most cases especially in the longer penetrations the rules sufficed to exclude all but one fit.

The direction of the electrode in the cortex, projected out into the visual field (we shall call this the "virtual" direction of the electrode), was next determined from the curve. The virtual track is perpendicular to the orientation for which the curve: change of orientation vs. distance travelled is steepest. The reasons are immediately obvious from Fig. 2a.

This done, we have two elements, the virtual direction of the electrode in the cortex and the orien-

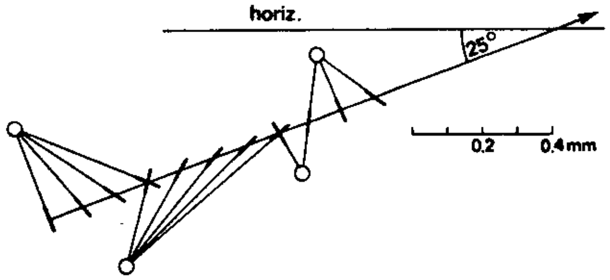

Fig. 8. Centers corresponding to the plot of Fig. 7. This reconstruction is possible only if the sphere of influence of the centers (notably the lowermost center of the diagram) is not assumed to be circularly symmetrical

tations encountered, which make it possible to reconstruct a map of the centers in the cortical plane. Strictly speaking, both elements are not known to us in terms of the cortical coordinates, but rather in terms of the coordinates of the visual field, and the map of the centers which we obtain will also be projected out in the visual field. However, the metric of this map is known from the known distances along the path of the electrode. The map is obtained simply by drawing the orientations onto the electrode track. Under the supposition of the scheme of Fig. 2a these orientations or rather the lines continuing them should meet in a smaller number of centers.

Figure 4 is intended to explain how an incorrect assumption on the (virtual) orientation of the electrode track will not reveal the centric arrangement of the orientations. Actually, another way of determining the virtual direction of the electrode from the orientation plots would be to minimize the number of points (in practice: small regions) in which the orientation lines intersect.

Finally, a theoretical curve was obtained from the map of the centers and this was compared to the experimental plots.

An example is shown in Fig. 5. This is the result of an analysis of Fig. 2a in Hubel and Wiesel (1974a). Our Fig. 6 shows the corresponding map of the centers, which is obtained assuming an angle of 67° between the (virtual) electrode track and the horizontal. The most difficult case is that of Fig. 3 in Hubel and Wiesel (1974a). Here the discontinuities lead to the assumption of a somewhat awkward position of the centers (our Figs. 7 and 8). Particularly challenging are the cases in which parallel penetrations were made. The reconstruction of the virtual direction of the electrode must be compatible with all individual plots, and when the penetrations are close together, common centers can be expected. Our Figs. 9 and 10 show the result of an analysis of the three parallel penetrations of Hubel and Wiesel's (1974a) Figs. 10 and 11. The fit is better if penetrations 2 and 3 are not staggered quite as much as the authors' sketch suggests. All other plots published in the same paper lead to quite straightforward reconstructions.

Turning to the cat (Albus, 1975b) one gains the impression of a somewhat more erratic architecture of orientation columns. Still, some long penetrations

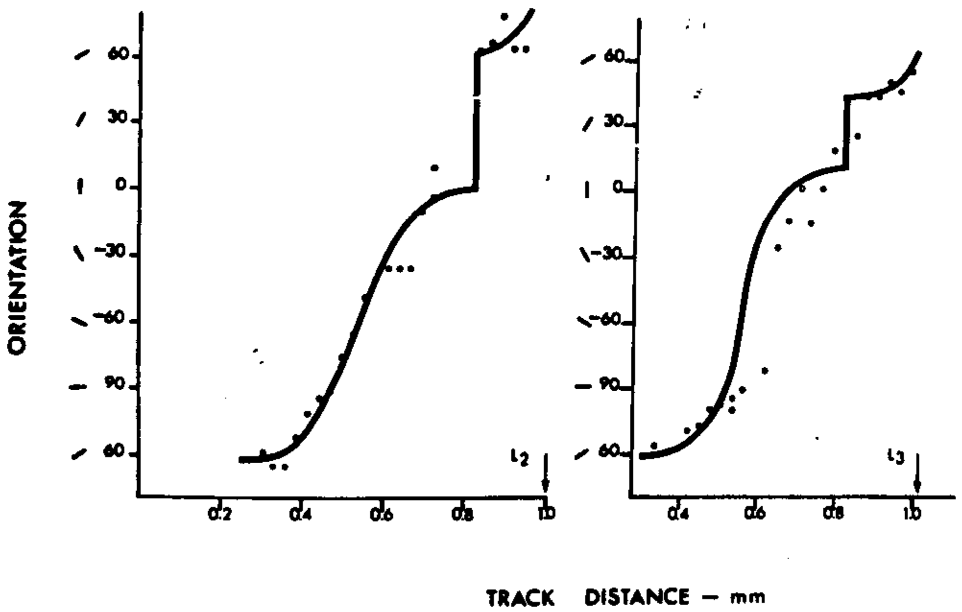

Fig. 9. From Hubel and Wiesel (1974a). Orientations recorded in two (P_2 and P_3) of three parallel penetrations. The curves are derived from the reconstruction of centers in Fig. 10

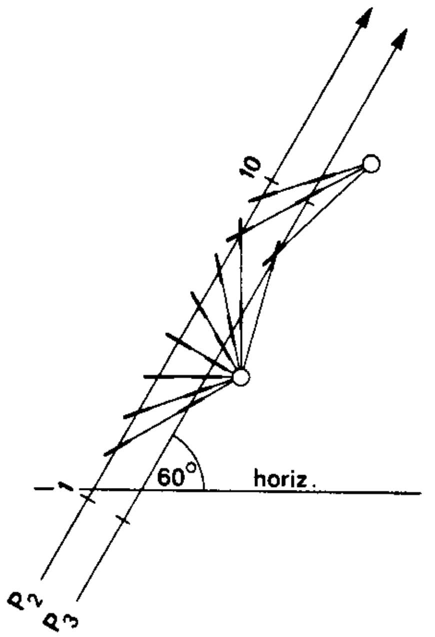

Fig. 10. Reconstruction of common centers for the penetrations P2 and P3 of Fig. 9. (P1 was parallel but far removed from P2 and P3 and could not be expected to have common centers with the others)

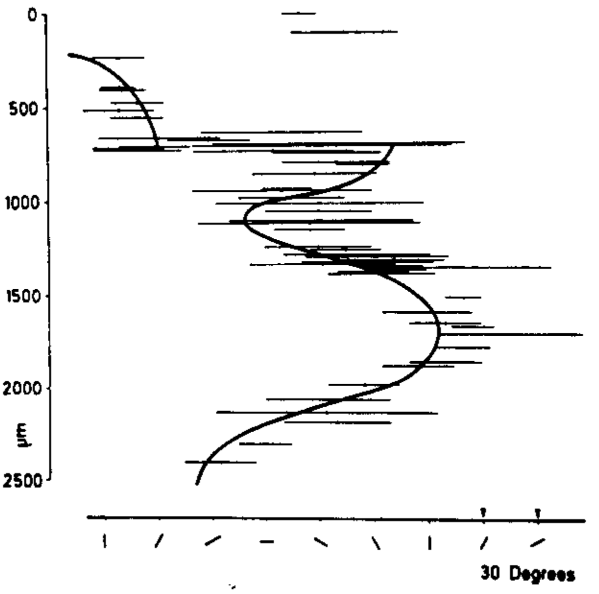

Fig. 11. From Albus (1975b). Note that here the diagram is rotated 90° with respect to the previous diagrams. The curve is derived from the reconstruction of centers in Fig. 12

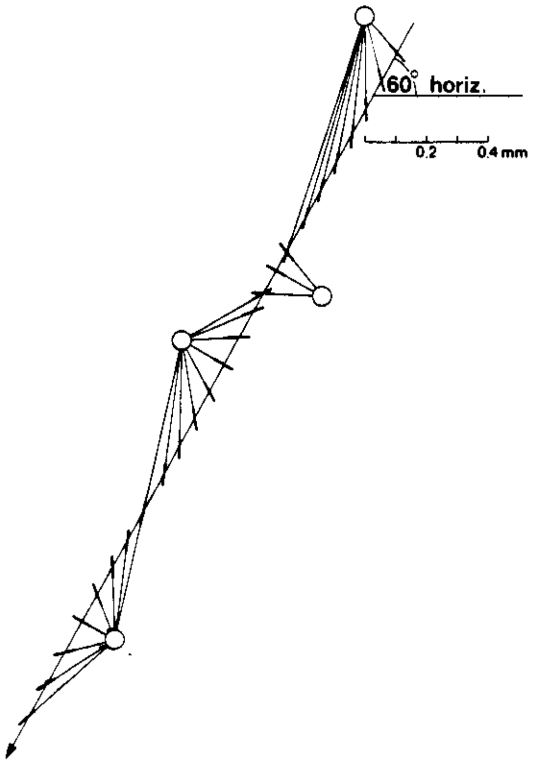

Fig. 12. Reconstruction of the centers corresponding to the plot of Fig. 11. Note the wider spacing of the centers in the case of the cat, compared to Figs. 6, 8, and 10 which refer to the monkey

(Albus, 1975b, Fig. 4) can be neatly matched by a map of centers (our Figs. 11 and 12) and the reward is provided by the match of the reconstructed virtual electrode path with the virtual electrode path actually recorded by the author. The particularly successful parallel penetrations of Albus (1975b) Fig. 7C and D led to the reconstruction of some common centers (our Fig. 13), even if the orientations seem much less strictly determined by them than in the case of the monkey.

Discussion

The verisimilitude of our interpretation rests on a feeling of neuroanatomical plausibility, as well as on the fairly good fit of our curves with the published plots. To impose centers seems a very natural way of creating a field of orientations in a continuum, and one than can be easily realized with the building blocks of the neuronal tissue. Suppose there are special large neurons appropriately spaced in the cortex. The orientation of the line detectors might be determined by fibers radiating out from these centers. Alternatively, thinking in terms of movement detectors rather than line detectors, we may suppose that the wiring is such that each neuron in the cortex responds to movement from the nearest special neuron to it. Since the optimal direction of movement for a cortical neuron is at right angles to the optimal orientation of a line, the two interpretations, radial orientations of lines vs. radial array of movement detectors, correspond to the two cases of Fig. 2a and b. The plots of orientations along a tangential traverse through the cortex could actually distinguish between the two cases if the virtual path of

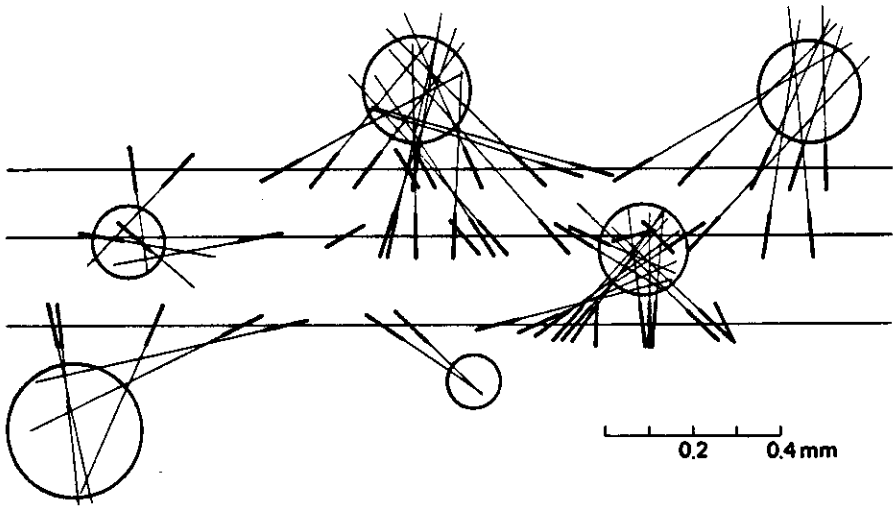

Fig. 13. Reconstruction of centers from three parallel penetrations made by Albus (1975b)

the electrode were also known, since the virtual electrode path reconstructed from the curves in one case is at right angles to what it would be in the other case. The match of our reconstructed electrode path with the electrode path actually recorded by Albus (his Fig. 4, our Fig. 11) speaks in favour of a radial orientation of line detectors, since it will be recalled it was Fig. 2a that we used as a working hypothesis for our reconstructions.

It is difficult to relate the geometry of orientation specificity to the cortical anatomy, since neither the properties of the elementary line (or movement-) detectors, nor the statistics of the intracortical connections are sufficiently well-known. It is tempting, however, to imagine the so-called giant cells described by Meynert in the place of the centers of our model. These are spaced, in the perifoveal monkey cortex (Chan-Palay et al., 1974), at distances of about 0.4 mm one from the other, corresponding very well to the distances between the centers which emerge from our reconstructions (e.g. on Fig. 6). The reconstructions from the cat experiments seem to yield larger distances between the centers (Fig. 12), which makes one think that the corresponding cellular elements in the cat are perhaps more widely spaced.

It would be premature to speculate in detail about the way in which Meynert cells impose either radial line detectors or radially orientated movement detectors. Radial axon collaterals of such a cell may train linear "cell assemblies" formed by neurons each of which would then appear as a line detector for that orientation. The radially oriented, very long basal dendrites of Meynert cells may also be part of a feedback loop involved in such a learning process. Or else, the giant cell of Meynert may serve as the low-pass filter connected to one of the inputs of a movement detector of the Reichardt-Hassenstein type [well known from work on the fly (Reichardt, 1970)], with surrounding, smaller pyramidal cells serving as the other input and as the coincidence detectors.

Direct experimental evidence for the localization and orientation of line (or movement) detectors may come from the staining of active nerve cells with radioactive deoxyglucose (Kennedy et al., 1976). The first attempt in this direction is not yet conclusive, since the distribution of radioactive label in the cortex induced by the presentation of a moving stripe pattern (Hubel et al., 1978) neither proves nor disproves the centric array of detectors. More disturbing to our model is a similar analysis in the tree shrew (Skeen et al., 1977) which resulted in a pattern that clearly does not suggest a centric array of orientations. It is quite possible that the tree shrew maps various parameters of the visual input onto the coordinates of the cortical plane in a way very different from cat and monkey. In fact, e.g. there are no ocular dominance columns in this animal.

The rich harvest of data in visual cortical physiology has attracted many theoreticians. Ideas cognate to our own have been advanced by various authors. The closest to our own conception is Seelen (1970) who proposed an array of orientations like that of our Fig. 2a at a time when the published records did not give it yet the support it has now. Other authors (Malsburg, 1973; Legendy, 1978) tend to make the almighty process of learning by coincidence of activity (through "Hebbian" synapses) responsible for the establishment of fields of neurons with continuously changing properties. In their view a certain orientation would not be a priori anchored in the cortical tissue, but finds its place through cooperative interaction. On the contrary, Finette et al. (1978) suppose, as we do, an anisotropy of the cortical network as being responsible for the orientation of the preferred line stimuli, but the idea of a centric pattern is not part of their theory. None of these theories is explicit enough to provide detailed explanations of particular experimental plots.

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