Orientation columns in macaque monkey visual cortex demonstrated by the 2-deoxyglucose autoradiographic technique

In the past fifteen years physiological studies of the primary visual cortex in higher mammals have provided evidence for two independent systems of functional subdivisions, ocular dominance columns and orientation columns. These two systems are closely related to two important functions of visual cortex: combining at a single-cell level the information that originates in the two eyes, and rearranging the spatial information from the lateral geniculate body so that cells after the initial stage of visual processing come to respond to specifically oriented lines in the visual field.

The ocular dominance columns have been demonstrated anatomically by three different staining techniques. We describe here the use of a new method which makes possible the anatomical demonstration of the orientation columns.

The original evidence that cells are aggregated according to their response characteristics came from microelectrode recordings. In a penetration perpendicular to the cortical surface all cells are dominated by the same eye and all give optimal responses to the same stimulus orientation, whereas in an oblique or tangential penetration there is an alternation of the dominant eye, from left to right and back, and, at the same time, a series of regular changes in optimal stimulus orientation in steps of 10° or less, clockwise or counterclockwise. Reversals in direction of rotation occur sporadically, on the average every few mm, and the orderly sequences of small orientation shifts are occasionally broken by abrupt large shifts of up to 90°. A full cycle of either type, one eye and then the other or a rotation through 180°, generally requires a horizontal movement along the cortex of 1 mm or less. The constancy of eye dominance and of optimal stimulus orientation during perpendicular penetrations indicates that the two sets of subdivisions are arranged perpendicular to the surface and the layers. Because of their cross-sectional shape in brain sections perpendicular to the surface, the subdivisions have been called 'columns', and a complete set of columns (left plus right eyes, or a full 180° rotation) is called a hypercolumn.

Inspection of cortical sections stained by conventional methods gives no hint of these vertical subdivisions. The only obvious segregation of cells is the horizontal system of layers, and this segregation has certain physiological correlates. Layer IVc, at about mid-cortical thickness, is the site of termination of the geniculate afferents and contains cells that differ in their physiological properties from cells in the other layers in two respects: like the geniculate afferents, they have no orientation preference; and they are almost all strictly monocular. In contrast, cells in the layers above and below IVc almost all show clear orientation specificity and about half are binocular, though any given cell is likely to respond best to one or the other eye.

In the last few years considerable progress has been made in working out the geometry of the columnar subdivisions. Three independent anatomical methods have made it possible to see the ocular dominance columns in layer IVc where they form a set of parallel bands which are for the most part straight, but in places form loops and whorls and occasionally show bifurcations and blind endings. The columns must therefore have the form of parallel sheets rather than being pillar-like. For the orientation columns.

and starch disappearance have been observed with stomatal opening. We have also found high levels of starch in guard cells of C. communis when stomata were closed; this level decreased as stomata opened although starch could still be detected at wide stomatal apertures. This suggests that there is a dynamic flux of carbon between malic acid and starch with the direction of starch production outpacing its breakdown when stomata are closing. Results of an investigation of pathways for malic acid–starch interconversions will be published elsewhere.

In conclusion we have established that malic acid is a precursor of starch synthesis in guard cells of C. communis. But, the mechanism of the control of guard cell CO₂ fixation and hence malic acid synthesis, and the control of the production of starch from malic acid in relation to stomatal movements, remain obscure.

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More superficial sections from this block, tangent to the upper layers (II–III) rather than to white matter, show an almost identical pattern, as expected from the fact that the labelled regions are perpendicular to the surface.

So far we have examined too few brains to be sure that the pattern of the orientation columns is always as complex in form as that shown here. Ocular dominance columns were examined in the same region as that shown in Fig. 2, by transneuronal autoradiography following an injection of 1H-proline into one eye two weeks before the deoxyglucose experiment. These showed a more regular pattern of stripes, with a spacing only slightly coarser than that of the orientation hypercolumns (770 μm compared with 570 μm). There was no obvious tendency for the two sets of columns to be related in any simple way: they were not consistently orthogonal, and were certainly not parallel. This result will be published separately.

The anatomical demonstration of the orientation columns provides still another verification of the columnar organisation of the striate cortex. It is reassuring to find such agreement between morphology and physiology, and unusual to find the physiology actually leading the way to a structural description.

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Instability of the eye
in the dark and proprioception

The extraocular muscles of most mammals contain stretch receptors which are not necessarily in the form of muscle spindles. The cat, for example, has no muscle spindles, but the oculomotor muscles contain structures, with spiral endings, that are in parallel with the muscle fibres and respond to stretch. Most proprioceptive fibres run extraocularly in the ophthalmic branch of the Vth nerve.1–4. The cell bodies of these fibres seem to be located in the mesencephalic root of the Vth nerve.5 There is electrophysiological evidence of proprioceptive projections to the cerebellum6–9, superior colliculus10 and visual cortex.9 The function of ocular proprioception is uncertain, although there is evidence that in man it may be an indicator of eye position in the dark.10 In the cat it seems to have a role in maintaining the binocularity of single neurones in the visual cortex11,12. Because most proprioceptive fibres run into the ophthalmic branch of the Vth nerve, we have investigated eye movements in the alert animal before and after section of this branch. We report here that, in the absence of visual and vestibular stimuli, the eye ipsilateral to the section becomes unstable and performs slow pendular oscillations. Asymmetries are observed in the horizontal vestibular nystagmus recorded in total darkness from the two eyes after unilateral section.

Cats chosen for their docility were anaesthetised with pentobarbital. A plastic cylinder was fixed to the skull and Ag–AgCl electrodes were implanted for recording horizontal movements of both eyes. The cat was trained to stay in a comfortable box with its head fixed by the plastic cylinder to a holder. The holder could either prevent any head motion or allow head rotations about a vertical axis. The cats were trained, over several days, to perform horizontal eye movements, tracking a visual target with the head either fixed or free to rotate horizontally. Eye movements were calibrated in each session by setting two pointers 30 cm from the eyes and displacing them 15° on either side of the cat's medial plane. The cat's attention was then called to either pointer while an experimenter checked the correctness of fixation, and the corresponding position of the recording trace was marked.

The cat box and the head holder were fixed to a table that could be oscillated sinusoidally about a vertical axis at various amplitudes and velocities.

When sufficient eye movements were recorded, the animal was again anaesthetised and the ophthalmic branch of the right Vth nerve was cut at the exit from the orbit or at the entrance into the semilunar ganglion. A small aperture was made into the parieto-temporal bone and the brain was lifted gently to reveal the three branches of the Vth nerve. Care was taken not to touch the oculomotor nerves. The operation was repeated on the left side after 2 or 3 weeks. After the experiments the animal was killed and the completeness of the section was checked.

We present here only results concerning eye movements in the dark, either spontaneous or elicited by head or body oscillations. The records of horizontal eye movements of normal cats that are awake in darkness contain periods with frequent spontaneous saccades, and periods with very few saccades, but with slow drifts mainly conjugate in the two eyes.

After section of the ophthalmic branch of the Vth nerve