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RECEPTIVE FIELDS, BINOCULAR INTERACTION AND FUNCTIONAL ARCHITECTURE IN THE CAT'S VISUAL CORTEX

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What chiefly distinguishes cerebral cortex from other parts of the central nervous system is the great diversity of its cell types and interconnexions. It would be astonishing if such a structure did not profoundly modify the response patterns of fibres coming into it. In the cat's visual cortex, the receptive field arrangements of single cells suggest that there is indeed a degree of complexity far exceeding anything yet seen at lower levels in the visual system.

In a previous paper we described receptive fields of single cortical cells, observing responses to spots of light shone on one or both retinas (Hubel & Wiesel, 1959). In the present work this method is used to examine receptive fields of a more complex type (Part I) and to make additional observations on binocular interaction (Part II).

This approach is necessary in order to understand the behaviour of individual cells, but it fails to deal with the problem of the relationship of one cell to its neighbours. In the past, the technique of recording evoked slow waves has been used with great success in studies of functional anatomy. It was employed by Talbot & Marshall (1941) and by Thompson, Woolsey & Talbot (1950) for mapping out the visual cortex in the rabbit, cat, and monkey. Daniel & Whitteridge (1959) have recently extended this work in the primate. Most of our present knowledge of retinotopic projections, binocular overlap, and the second visual area is based on these investigations. Yet the method of evoked potentials is valuable mainly for detecting behaviour common to large populations of neighbouring cells; it cannot differentiate functionally between areas of cortex smaller than about 1 mm^2. To overcome this difficulty a method has in recent years been developed for studying cells separately or in small groups during long micro-electrode penetrations through nervous tissue. Responses are correlated with cell location by reconstructing the electrode tracks from histological material. These techniques have been applied to

the somatic sensory cortex of the cat and monkey in a remarkable series of studies by Mountcastle (1957) and Powell & Mountcastle (1959). Their results show that the approach is a powerful one, capable of revealing systems of organization not hinted at by the known morphology. In Part III of the present paper we use this method in studying the functional architecture of the visual cortex. It helped us attempt to explain on anatomical grounds how cortical receptive fields are built up.

METHODS

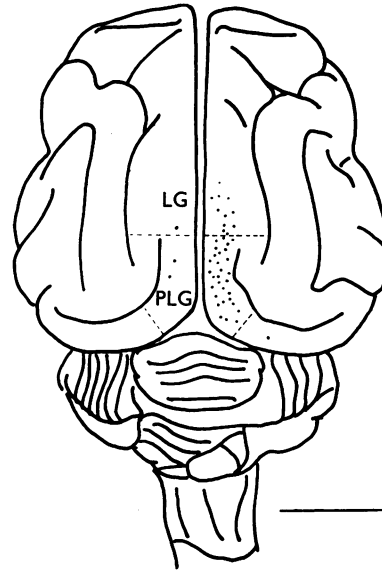
Recordings were made from forty acutely prepared cats, anaesthetized with thiopental sodium, and maintained in light sleep with additional doses by observing the electrocorticogram. Animals were paralysed with succinylcholine to stabilize the eyes. Pupils were dilated with atropine. Details of stimulating and recording methods are given in previous papers (Hubel, 1959; Hubel & Wiesel, 1959, 1960). The animal faced a wide tangent screen at a distance of 1·5 m, and various patterns of white light were shone on the screen by a tungsten-filament projector. All recordings were made in the light-adapted state. Background illumination varied from $-1{\cdot}0$ to $+1{\cdot}0$ $\log_{10}$ cd/m^2. Stimuli were from 0·2 to 2·0 log. units brighter than the background. For each cell receptive fields were mapped out separately for the two eyes on sheets of paper, and these were kept as permanent records.

Points on the screen corresponding to the area centralis and the optic disk of the two eyes were determined by a projection method (Hubel & Wiesel, 1960). The position of each receptive field was measured with respect to these points. Because of the muscle relaxant the eyes usually diverged slightly, so that points corresponding to the two centres of gaze were not necessarily superimposed. In stimulating the two eyes simultaneously it was therefore often necessary to use two spots placed in corresponding parts of the two visual fields. Moreover, at times the two eyes were slightly rotated in an inward direction in the plane of their equators. This rotation was estimated by (1) photographing the cat before and during the experiment, and comparing the angles of inclination of the slit-shaped pupils, or (2) by noting the inclination to the horizontal of a line joining the area centralis with the optic disk, which in the normal position of the eye was estimated, by the first method, to average about 25°. The combined inward rotations of the two eyes seldom exceeded 10°. Since the receptive fields in this study were usually centrally rather than peripherally placed on the retina, the rotations did not lead to any appreciable linear displacement. Angular displacements of receptive fields occasionally required correction, as they led to an apparent difference in the orientation of the two receptive-field axes of a binocularly driven unit. The direction and magnitude of this difference were always consistent with the estimated inward rotation of the two eyes. Moreover, in a given experiment the difference was constant, even though the axis orientation varied from cell to cell.

The diagram of Text-fig. 1 shows the points of entry into the cortex of all 45 microelectrode penetrations. Most electrode tracks went no deeper than 3 or 4 mm, so that explorations were mainly limited to the apical segments of the lateral and post-lateral gyri (LG and PLG) and a few millimetres down along the adjoining medial and lateral folds. The extent of the territory covered is indicated roughly by Text-figs. 13–15. Although the lateral boundary of the striate cortex is not always sharply defined in Nissl-stained or myelin-stained material, most penetrations were well within the region generally accepted as 'striate' (O'Leary, 1941). Most penetrations were made from the cortical region receiving projections from in or near the area centralis; this cortical region is shown in Text-fig. 1 as the area between the interrupted lines.

Tungsten micro-electrodes were advanced by a hydraulic micro-electrode positioner (Hubel, 1957, 1959). In searching for single cortical units the retina was continually stimulated with stationary and moving forms while the electrode was advanced. The unresolved background activity (see p. 129) served as a guide for determining the optimum stimulus. This procedure increased the number of cells observed in a penetration, since the sampling was not limited to spontaneously active units.

In each penetration electrolytic lesions were made at one or more points. When only one lesion was made, it was generally at the end of an electrode track. Brains were fixed in 10% formalin, embedded in celloidin, sectioned at 20 μ, and stained with cresyl violet. Lesions were 50–100 μ in diameter, which was small enough to indicate the position of the electrode tip to the nearest cortical layer. The positions of other units encountered in a cortical penetration were determined by calculating the distance back from the lesion along the track,



Text-fig. 1. Diagram of dorsal aspect of cat's brain, to show entry points of 45 micro-electrode penetrations. The penetrations between the interrupted lines are those in which cells had their receptive fields in or near area centralis. LG, lateral gyrus; PLG, post-lateral gyrus. Scale, 1 cm.

using depth readings corresponding to the unit and the lesion. A correction was made for brain shrinkage, which was estimated by comparing the distance between two lesions, measured under the microscope, with the distance calculated from depths at which the two lesions were made. From brain to brain this shrinkage was not constant, so that it was not possible to apply an average correction for shrinkage to all brains. For tracks marked by only one lesion it was assumed that the first unit activity was recorded at the boundary of the first and second layers; any error resulting from this was probably small, since in a number of penetrations a lesion was made at the point where the first units were encountered, and these were in the lower first or the upper second layers, or else at the very boundary. The absence of cell-body records and unresolved background activity as the electrode passed through subcortical white matter (see Text-fig. 13 and Pl. 1) was also helpful in confirming the accuracy of the track reconstructions.