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VISUAL AREA OF THE LATERAL SUPRASYLVIAN GYRUS (CLARE–BISHOP AREA) OF THE CAT

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SUMMARY

On anatomical and physiological grounds a zone of cat cortex deep in the medial bank of the suprasylvian sulcus (the Clare–Bishop area) is known to receive strong visual projections both from the lateral geniculate body and area 17. We have mapped receptive fields of single cells in this area in eight cats.

Active responses to visual stimuli were found over most of the medial bank of the suprasylvian sulcus extending to the depths and over to the lowest part of the lateral bank. The area is clearly topographically arranged. The first responsive cells, recorded over the lateral convexity and 2–3 mm down the medial bank, had receptive fields in the far periphery of the contralateral visual fields. The receptive fields tended to be large, but showed considerable variation in size and scatter in their positions. As the electrode advanced down the bank, fields of successively recorded cells gradually tended to move inwards, so that in the depths of the sulcus the inner borders of many of the fields reached the vertical mid line. Here the fields were smaller, though they still varied very much in size.

Receptive fields were larger than in 17, 18, or 19, but otherwise were not obviously different from the complex and lower-order hypercomplex fields in those areas. No simple fields, or concentric fields of the retino-geniculate type, were seen. Cells with common receptive-field orientation were grouped together, but whether or not the grouping occurs in columns was not established.

Most cells were driven independently by the two eyes. Fields in the two eyes seemed to be identical in organization. Cells dominated by the contralateral eye were much more common than ipsilaterally dominated ones, but when cells with parafoveal and peripheral fields were considered separately, the asymmetry was seen to apply mainly to cells with peripheral fields.

INTRODUCTION

In 1943, Marshall, Talbot & Ades, while recording the responses of cat cortex to visual stimulation, observed evoked activity in a region close to the suprasylvian sulcus, some distance from the classical visual receiving areas. They could not abolish the response by making lesions in the lateral gyrus, and concluded that the area received projections from the lateral geniculate body or structures close to the geniculate. Over a decade later Clare & Bishop (1954) narrowed the responsive zone down to a strip of cortex deep within the suprasylvian sulcus, lying along its medial lip (Fig. 1). The responses were evoked by stimulating either the optic nerve or the lateral gyrus of the cortex (presumably areas 17 and 18 of Otsuka & Hassler (1962)).

Over the past few years anatomical studies have also implicated this same suprasylvian region as part of the visual system. Nauta methods have demonstrated projections to it from the lateral geniculate body (Glickstein, King, Miller & Berkley, 1967; Wilson & Cragg, 1967); from area 17 of either side (Hubel & Wiesel, 1965; Wilson, 1968); and from areas 18 and 19 of either side (Wilson, 1968). Removal of cortex lateral to areas 17, 18 and 19 gives by itself minimal retrograde degeneration in the lateral geniculate body (Sprague, 1966); to produce complete degeneration one must destroy these more lateral areas as well as 17, 18 and 19 (Garey & Powell, 1967). There is thus anatomical and physiological evidence for projections to the lateral suprasylvian region from the lateral geniculate body and from 17, 18, and 19.

By studying responses of single cells to restricted spots and patterns of light, we have recently identified three distinct cortical visual areas in the cat (visual areas I, II, and III), and found them to be identical with architectonically defined areas 17, 18 and 19 of Otsuka & Hassler (1962). It seemed natural to extend this work by exploring the suprasylvian region, and the present paper represents a beginning in this direction. Cells in the area are easily influenced by visual stimuli, and their receptive fields are in many ways similar to those in 17, 18, and 19. The region is topographically ordered. We have seen little evidence that the analysis of form is carried further in this region, and so far its physiological significance remains a puzzle.

METHODS

Methods for stimulating and recording have been described in previous papers (Hubel & Wiesel, 1962, 1965), and will only be summarized here. A cat was anaesthetized with intraperitoneal thiopental, given intravenous succinylcholine to paralyse the eye muscles, and artificially respirated. Light anaesthesia was maintained throughout the experiment. The animal was placed in a stereotaxic head holder, and the eyes fitted with contact lenses

to obtain a focus upon a screen at a distance of 1·5 m. Stimuli consisted of stationary and moving patterns of light projected against a diffuse photopic background. A tungsten micro-electrode was advanced hydraulically in a closed-chamber system, and several electrolytic lesions were made in each penetration. For track reconstruction all brains were fixed in formalin, embedded in celloidin, sectioned at 25 μ, and stained with cresyl violet.

Experiments were done in eight adult cats. The micro-electrode was inserted into the lateral part of the suprasylvian gyrus, at about Horsley–Clark level A4 to A6, and lowered along the medial bank of the suprasylvian sulcus. The regions explored consisted of the medial bank to the depths of the sulcus, and part way round to include the lowest part of the lateral bank.

RESULTS

Brisk activity was seen in response to visual stimulation either on first entering the suprasylvian gyrus or after descending about one-third of the way along its lateral bank (Fig. 1). As in 17, 18, and 19, diffuse light gave

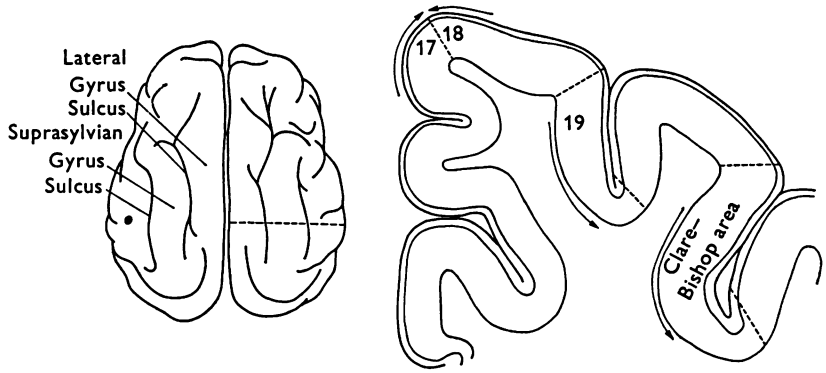

Fig. 1. Diagram of cat brain, as seen from above (anterior is up) and in coronal section, defining topographical terms used in this paper. For each of four topographically organized regions, arrows are directed from peripheral representation towards mid line representation.

virtually no responses, but line stimuli (slits, dark bars, and edges) were very effective over restricted regions. For optimum response the stimulus orientation was also critical, varying from cell to cell, and a moving stimulus was usually much more effective than a stationary one. About two thirds of the cells were 'complex', and the remainder 'hypercomplex' (Hubel & Wiesel, 1965). No 'simple' cells were seen. Hypercomplex cells were almost all of lower order. There was little suggestion that the kinds of form analysis occurring in 19 or even in 17 are carried further in the Clare–Bishop region.

Perhaps the main distinguishing feature of this area was the large size, and the great variation in size, of the receptive fields. On the average the fields even exceeded those of 18 in the territory they occupied, often taking up most of a visual-field quadrant. A second, less conspicuous

difference concerned the responses to moving lines. As in 17, 18, and 19, the best responses were obtained to optimally oriented lines swept across the receptive field, and the responses were either about equal, for movements in the two diametrically opposite directions, or were very unequal. In the Clare–Bishop area cells strongly preferring one direction over the opposite were about three times as numerous as those showing no preference, in contrast to the more nearly equal representation of the two groups in 17, 18, and 19. To give an extreme example, in one penetration, described below (Fig. 3), only three out of thirty-two cells responded equally well to an optimally oriented slit moved in the two opposite directions.

Simultaneously recorded cells always had the same receptive-field orientation, and this was also usually true of successively recorded cells (see Fig. 3, below). Moreover, the orientation that was most effective for a given cell was also most effective for any unresolved activity audible in the background. There thus seems little doubt that cells of common receptive field orientation are grouped, as they are in 17, 18, and 19. We still lack compelling evidence that the groupings are in the form of columns, evidence such as comparisons between normal and tangential penetrations, lesions at points of transition in orientation in multiple parallel penetrations, or surface maps. Nevertheless, a columnar system seems a very likely possibility.

Ocular dominance. Most cells were driven independently from the two eyes. As in areas 17–19 there were no obvious differences in the field structure of a single cell in the two eyes, either in orientation, position, or optimal stimulus (Hubel & Wiesel, 1962, 1965). No thorough search was made for horizontal disparity in field positions. As in other areas, the ocular dominance varied from cell to cell. The relative abundance of cells in the different ocular dominance groups varied depending on the position of the fields, and hence in the region of the suprasylvian gyrus from which recordings were made. Figure 2*A* shows the ocular dominance distribution for cells having fields within 10° of the area centralis. This histogram resembles those previously obtained for cells in 17, 18, and 19 (Hubel & Wiesel, 1965) most of which likewise had centrally located fields, for reasons having to do with sampling. Cells whose field centres were further out than 10° tended strongly to favour the contralateral eye, as shown by the histogram of Fig. 2*B*. The surprisingly large number of group 1 cells (those responding only to the contralateral eye) would be even larger if it included cells whose fields were in the extreme periphery of the visual field, beyond the region of overlap of the two eyes.

Topography, field size, and scatter. All the experiments showed a clear but rather crude topographic representation of the contralateral field of vision. Two typical examples are shown in Figs. 3 and 4. In the experiment

of Fig. 3 the first responsive cells were found at point *a* (Fig. 3*A*). Fields of the twelve cells recorded between *a* and *b* were scattered over a region below the horizontal meridian, extending out 20–50 from the vertical mid line. These fields are shown diagrammatically superimposed in Fig. 3*B*. As the electrode advanced, the fields tended to be situated closer and closer to the mid line, so that by mid-penetration, between points *b* and *c*

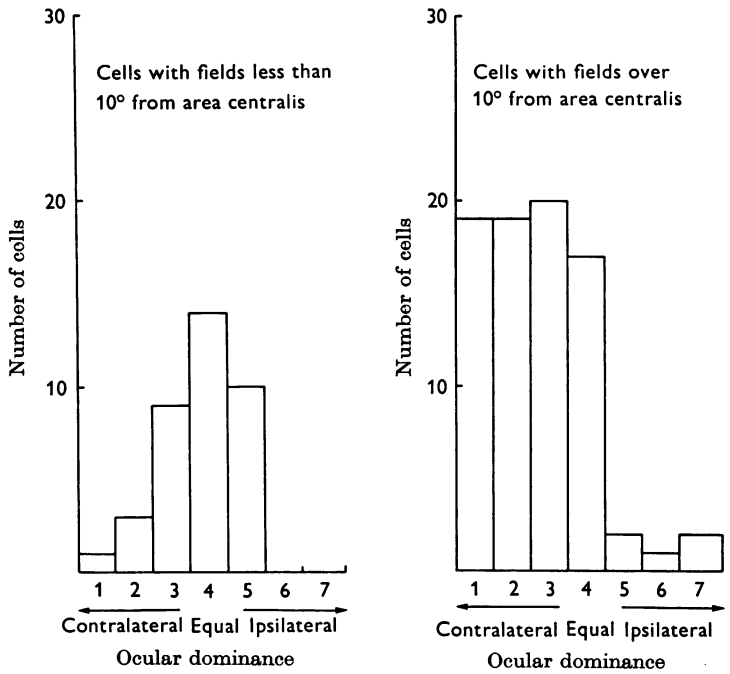

Fig. 2. Histograms showing distribution of cells according to ocular dominance. Cells with field centres within 10° of the area centralis are plotted separately from those with more peripheral fields. Cells of group 1 were driven only by the contralateral eye; for cells of group 2 there was marked dominance of the contralateral eye, for group 3, slight dominance. For cells in group 4 there was no obvious difference between the two eyes. In group 5 the ipsilateral eye dominated slightly, in group 6, markedly; and in group 7 the cells were driven only by the ipsilateral eye.

(Fig. 3*C*), they were centred some 10–15° out, and in the deepest part of the penetration, between *c* and *d* (Fig. 3*D*), they had moved in to within a few degrees of the vertical mid line. A graph summarizing the inward trend of field centres with electrode depth is given in Fig. 3*A*.

In the second example, illustrated in Fig. 4, responsive cells were recorded from the outset of the penetration. In this Figure the horizontal lines represent the horizontal extent of each field, and the short vertical marks indicate either the geometric centre or the region from which

strongest responses were evoked. The first cells had fields that reached beyond 70° from the mid line. Again the inward trend with increasing depth was clear, though over any small segment of the penetration it tended to be masked by the large variation in field size and the scatter in position, up-and-down as well as mediolateral. Just as was seen in 17, 18, and 19, the scatter in field-centre position was roughly the same as the size of the largest fields.

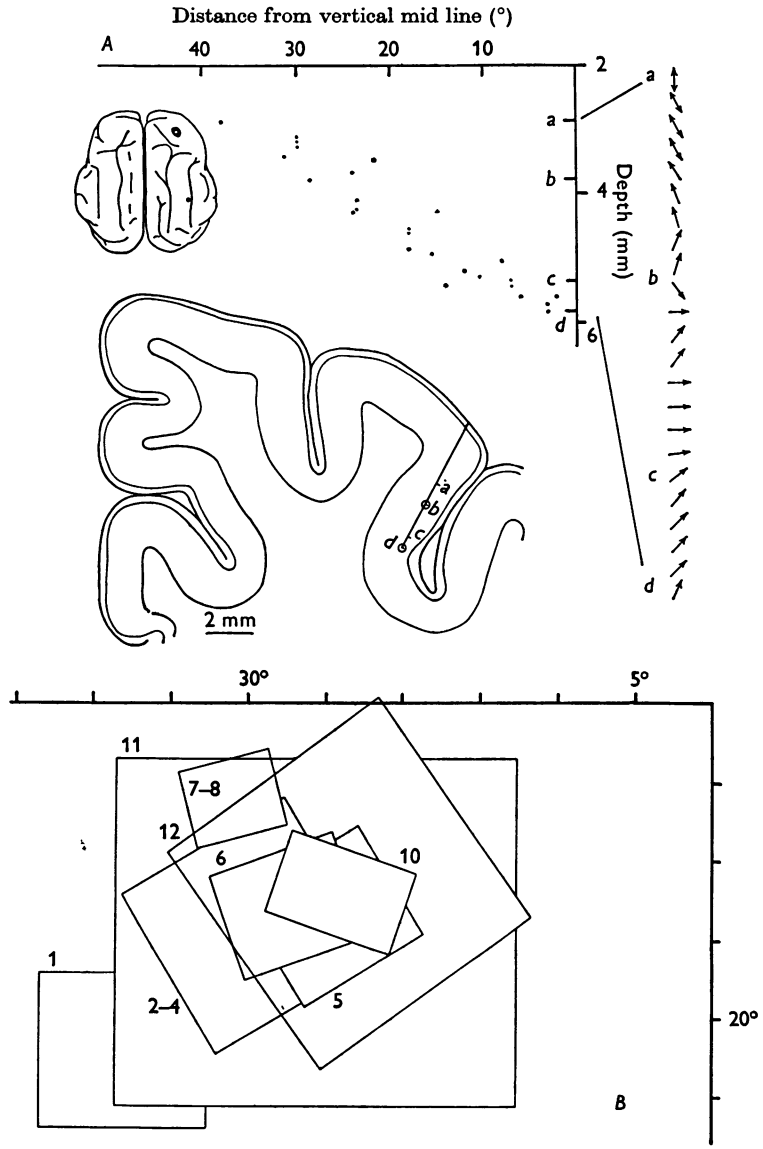

Fig. 3. For legend see opposite page.

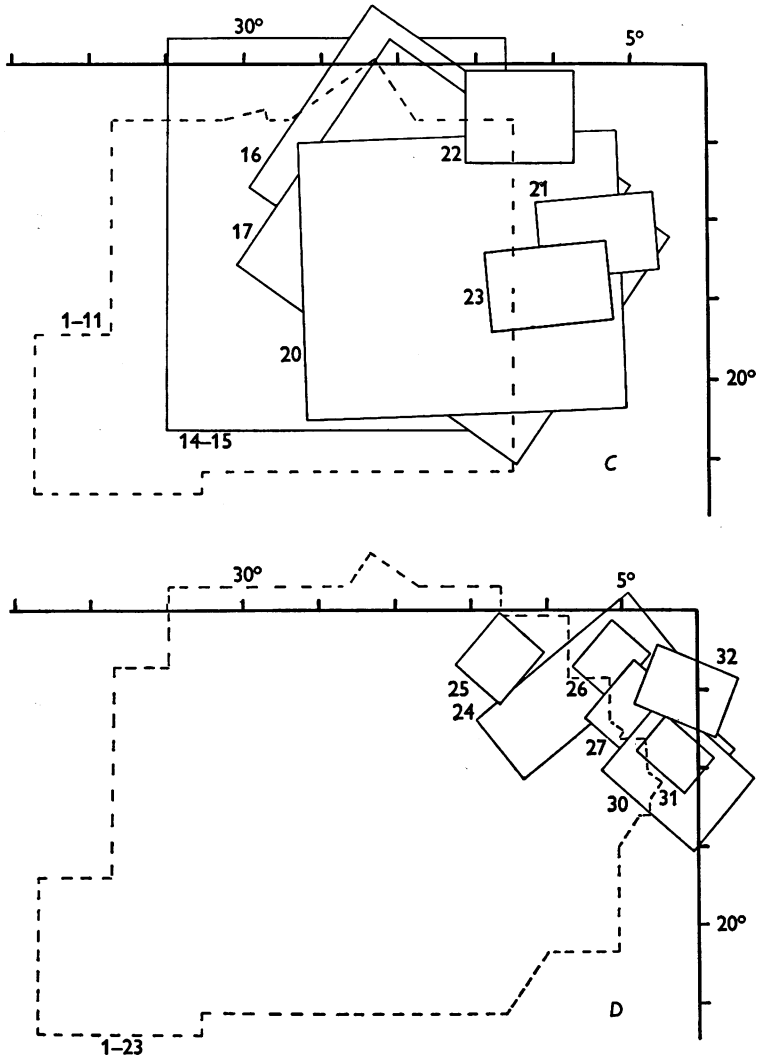

Fig. 3. Reconstruction of a penetration through most of the lateral bank of the suprasylvian gyrus. Point of entry is marked by a dot in inset of Fig. 3*A*. Lesions indicated by circles were made at *b* and *d*. First responsive cells were recorded at point *a*, at a depth of about 3 mm; here fields were 30–40° out in the contralateral periphery, below the horizontal meridian. Fields of cells recorded between *a* and *b* are illustrated in Fig. 3*B*, those recorded between *b* and *c* in 3*C*, and between *c* and *d* in 3*D*. The dotted lines in Fig. 3*C* and 3*D* represent the area taken in by receptive fields of the preceding diagrams. In the upper right part of Fig. 3*A* positions of field centres are plotted against electrode depth. Receptive field orientations are indicated to the right of the graph.

All experiments gave similar results, with fields in the upper part of the bank far in the periphery, and those deep in the sulcus close to the mid line. At the antero-posterior levels explored, most fields were centred below the horizontal meridian: presumably the superior visual fields are represented more posteriorly in the cortex, just as they are in 17, 18, and 19, but this was not investigated.

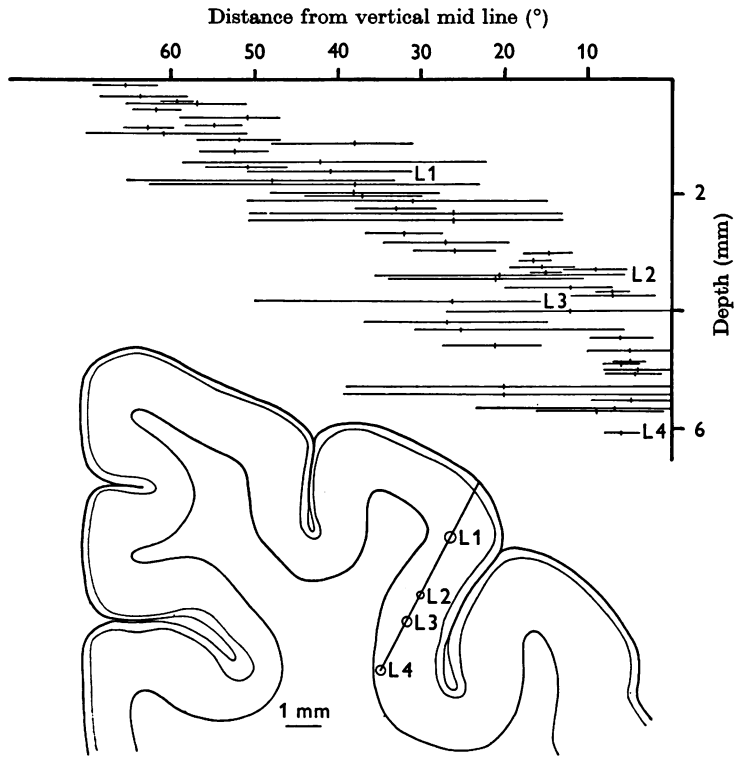

Fig. 4. Reconstruction of a penetration in the lateral bank of the suprasylvian gyrus. Circles (L 1–L 4) represent four electrolytic lesions made along the electrode trajectory. In the graph the horizontal lines show the mediolateral extent of the receptive fields, and the short vertical lines indicate either the geometrical centre or the area from which responses were maximal.

On the average, fields close to the area centralis were much smaller than those in the periphery. This was seen in most experiments, and is well shown in Fig. 3*B*, *C*, and *D*. The tendency was less obvious in the experiment of Fig. 4, which was exceptional in this respect.

Many of the fields bordered on the vertical mid line, some of them extending into the ipsilateral field for several degrees. This overlap across the mid line presumably reflects the input the area receives from area 17 of the opposite hemisphere, and hence, ultimately, from the ipsilateral

visual field. A similar overlap has been seen in recordings from 18 (Hubel & Wiesel, 1967).

DISCUSSION

When one compares this lateral suprasylvian area with areas 17, 18, and 19, the similarities are far more marked than the differences. The preference for precisely oriented lines, especially lines moving through the visual field, the presence of asymmetric responses to the two opposite directions of movement of an optimally oriented line, and the topographic representation with staggering in field position, all are common to all four cortical regions. So far, receptive fields in the Clare–Bishop area seem roughly similar to those in the other three areas, except that there are no simple cells of the type seen in 17, and fewer higher-order hypercomplex cells than in 19, if indeed there are any at all.

The main differences between this area and the other three lie in the enormous size of many of the fields, the variability in size, and the correspondingly large scatter in field positions. In the coarseness of representation implied by the large fields and wide scatter this area exceeds 18, just as 18 exceeds 17 and 19. It is as though many of the same processes were taking place in the Clare–Bishop area and in 18, in parallel fashion, but with different degrees of refinement.

A paper recently published by Sterling & Wickelgren (1968) gives a description of cells in the cat optic tectum, studied by methods similar to the ones used here. The authors showed that although tectal cells resemble cortical cells in many respects they are also in many respects different, particularly in not responding specifically to lines, in being relatively insensitive to orientation of contours, and in strongly preferring movement away from the mid line of the visual fields. The Clare–Bishop area thus seems much more akin to the other cortical areas than to the tectum. One reason for emphasizing the contrast between the tectum on the one hand and 18 or the Clare–Bishop area on the other concerns the dual projections that each of these receives: the tectum from the optic nerve and the 17, 18, 19 complex; 18 and the Clare–Bishop area from the geniculate and from 17, 18, and 19. In the optic tectum Wickelgren & Sterling (1968) showed that the more complex properties, e.g. the preferred direction of movement and much of the binocular convergence, disappear when the 17–19 complex is ablated; how the optic nerve contributes to the responses of the normal tectum is still not clear. For the Clare–Bishop area we found in one experiment that the responses similarly disappear on removal of 17, 18, and 19, but retrograde degeneration in the geniculate makes this result difficult to interpret. Thus, the question of the relative contributions of 17, 18 and 19 and the geniculate to the suprasylvian visual area still remains to be answered.

We are left, finally, with the puzzling prospect of an area for which we can, in our present state of knowledge, assign no obvious function. The main object of this study was to verify the existence of a region separate from the classical areas and strongly concerned with vision, to determine at least some properties of the cells, and to establish roughly the topographic organization, if any. A better understanding of its function, however, will require much more work on the receptive fields, and especially, perhaps, a comparison of the properties of cells in different layers. Some idea of where this region projects would also be useful.

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