CORTICAL AND CALLOSAL CONNECTIONS
CONCERNED WITH THE VERTICAL MERIDIAN
OF VISUAL FIELDS IN THE CAT

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In higher mammals the left half of the visual field is represented in the right visual cortex, and the right half in the left cortex. The fact that our visual fields appear uniform, with no obvious interruption along the vertical midline, would seem to call for connections linking the two hemispheres. The present paper deals with the physiological properties of some of these connections.

In the cat the vertical midline of the visual field has its primary representation in and close to the poorly defined boundary between areas 17 and 18 (7, 10). Each half-visual field is represented in both 17 and 18 in mirror fashion, so that as one proceeds away from the 17-18 boundary in either direction, medially along 17 or laterally along 18, the corresponding region of visual fields moves outward from the vertical meridian into the contralateral visual field. Recent anatomical evidence indicates that the part of area 17 adjacent to the 17-18 boundary sends callosal projections to the other hemisphere, ending in 18 near the 17-18 boundary (2, 7, 8) and possibly also in the adjacent part of 17 (8). Thus the parts of 17 and 18 having to do with the vertical midline of the visual fields are apparently connected on the two sides by the corpus callosum. In contrast, the more medial parts of 17, representing the peripheral parts of the visual fields, seem not to be reciprocally interconnected, and indeed one would hardly expect that cells concerned with a particular part of the left visual field should be connected specifically to cells concerned with the corresponding region in the right field.

These anatomical findings have lately been confirmed in the elegant physiological experiments of Choudhury, Whitteridge, and Wilson (1). They showed that with one optic tract cut, responses to light could be evoked in the ipsilateral hemisphere only near the 17-18 border, and only when the stimulus was applied near the vertical meridian. The responses were abolished either by cooling the corresponding region in the contralateral hemisphere or by cooling or cutting the posterior corpus callosum.

Several lines of evidence thus indicate that fibers in the corpus callosum originating in the most lateral part of 17 and projecting to 18 on the other side have special functions involving the vertical midline of the visual field.

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If this is so, then some cells in 18 near the 17–18 boundary ought to have receptive fields that straddle the vertical midline. Experimentally this is difficult to verify directly, since in the cat the exact position of the vertical midline is not easy to establish. Our first objective was to circumvent the difficulty by making simultaneous recordings from visual areas in the two hemispheres, looking for possible overlap between receptive fields of cells on the two sides. Any overlap would of course mean that at least one of the two receptive fields extended across the vertical meridian. A second objective was to record fibers directly from the corpus callosum, examine their responses to visual stimulation, and see to what extent they are preoccupied with the vertical midline.

METHODS

The experimental preparation was similar to that used in our previous work (4–6). The cat was anesthetized with intraperitoneal thiopental, the head held in a Horsley-Clarke stereotaxic apparatus, the eyes paralyzed with intravenous succinylcholine and held open facing a white tangent screen at a distance of 1.5 m. Pupils were dilated with homatropine, and the corneas protected with contact lenses. The focus of images on the screen was determined with a slit retinoscope, and if necessary adjusted by interposing spherical lenses. Positions on the screen corresponding to the area centralis and optic disc of each eye were determined by using an opthalmoscope (4), and the points were remeasured every hour or so, or whenever there was suspicion that the eyes had moved. Stimuli consisted of black or white lines or edges projected against a diffuse white background (6).

Cortical recordings were made with two independently positioned tungsten electrodes connected to separate recording channels. The electrodes were introduced through small holes in the skull and dura 1–2 mm to either side of the midline at the same Horsley-Clarke level. The corpus callosum was explored between planes A2 and A6 with a single electrode inserted stereotaxically 1–2 mm to the left or right of the midline. In all penetrations electrolytic lesions were made to identify the electrode tracks by passing 1–5 μA for 5–10 sec (4).

RESULTS

Simultaneous recordings from the two hemispheres

An exploration was first made of the cortical representation of the vertical midline of the visual field, looking especially in 17 and 18 for any possible overlap between the two half fields across the midline. Five such experiments were done. In each of these, two electrodes were placed initially in roughly corresponding parts of the postlateral gyrus, close to the region representing the area centralis (Horsley-Clarke frontal plane −2 to +1). Receptive-field positions were mapped for several cells in each hemisphere, and if necessary one electrode was moved forward or back until the fields were at about the same horizontal level.

In the experiment of Fig. 1A one penetration was made on the left side and three on the right. Both electrodes were in area 17, close to the 17–18 border. Some fields of simultaneously recorded cells touched, but in no case was there a common region of visual field within which a stimulus excited cells in both hemispheres simultaneously. Cells 2 and 6, whose fields might seem to overlap, were studied some time apart, and it is possible that small eye movements may have occurred in the interval. Because of the imprecise...
Fig. 1. Receptive fields of cells plotted in simultaneous recordings from the two hemispheres. Fields outlined by interrupted lines correspond to cells in the left hemisphere; continuous lines, right hemisphere. AC = area centralis. A: one penetration was made in the left hemisphere (L) and three (P1-P3) in the right (R), at different anteroposterior levels. All penetrations were in 17, close to the 17-18 border. Simultaneous recordings were made of units 1 (R) and 2 (L); then 4 (R) and 2 (L); then 4 (R) and 5 (L); and finally 6 and 7 (R) together with 5 (L). In none of these simultaneous recordings was there any trace of overlap. B: a similar experiment in which the left electrode was in 17 and the right in the transition zone between 17 and 18. Unit 2 recorded simultaneously with 3 and then with 4; unit 4 recorded simultaneously with 5 and then 6.

sion in estimating the exact center of gaze, the vertical meridian in all these figures is only a rough estimate, to the nearest degree or so.

Two other experiments also failed to show a convincing overlap across the midline. In one of these, both electrodes again were in 17; in the other (Fig.
FIG. 2. A: fields of cells recorded with two electrodes in the 17-18 transition zone on the two sides, showing overlap across the midline. Upper sequence: simultaneous recordings made of cells 1 and 2, 2 and 3, 3 and 4. Lower sequence: 9, 10, and 11 recorded simultaneously; then 10, 11 and 12. B (opposite page): same experiment, all fields from the two penetrations shown superimposed. Fields of cells from the right hemisphere are outlined by continuous lines; from left hemisphere, by interrupted lines.
one electrode was in 17 and one in the transitional region between 17 and 18.

In two of the five experiments there was clear overlap between fields of cells on the two sides. In the first animal one electrode was in 17 and the other in 18. In the second experiment, illustrated in Fig. 2, both electrodes were in the 17–18 transitional zone. The field maps of Fig. 2 were obtained by first advancing one electrode and then the other, making a number of simultaneous recordings. In Fig. 2A the two maps correspond to two sets of simultaneously recorded cells. In the upper set cells 1 and 2 were studied together, then 3 and 2, and then 3 and 4, one electrode always being kept in place while the other was advanced, to be sure that the eyes had not moved in the meanwhile. Similarly for the lower set, cell 9 was recorded from the left hemisphere together with units 10 and 11 on the right; then the left electrode was advanced and cell 12 was observed together with 10 and 11. In both these sets the stimulus could be moved strictly within the region of overlap while the responses of the two cells were observed.

The fields of all 22 cells recorded in this experiment are shown superimposed in Fig. 2B. Eleven cells were recorded from the right hemisphere (continuous lines) and 11 from the left (interrupted lines). By always having a cell under observation in one hemisphere or the other we could be certain that there were no eye movements of more than about 1/4°. As usual in studies of visual cortex, the total visual-field area occupied by the over-
lapping receptive fields of a group of cells in a small region of cortex was two to four times that of an average receptive field in the group. The two groups of receptive fields from the two hemispheres themselves overlapped over about 1/3 of their total area.

Correspondence of receptive-field position in binocularly driven cells. The following observations have little direct bearing upon the problem of midline overlap of receptive fields, but were made incidentally while recording from pairs of cells simultaneously with two electrodes. The two receptive fields of a binocularly driven cell are known to occupy corresponding positions in the two retinas, at least to within a degree or so (6). Obviously, any slight departures from correspondence from one cell to the next would be of great interest, especially if one found a variation in the horizontal direction and not in the vertical, for this would suggest that some cells were specialized to respond to images of objects in front of or behind some surface of reference determined by the degree of convergence of the two eyes. Whether a cell's two receptive fields always correspond precisely in position has been hard to judge, because the position of the area centralis cannot be accurately determined by ophthalmic inspection. Moreover, the relative positions of the receptive fields in the two eyes as one proceeds from cell to cell often seem to vary slightly, but it is difficult to evaluate this apparent variation because of occasional small eye movements. The problem of eye movements can be overcome in double recordings by keeping one binocularly driven cell under observation at all times and noting any change of position of either of the projected receptive fields.

In the experiment of Fig. 3, recordings were made from area 17 on the two sides. Here the receptive fields are shown just as they were mapped on the projection screen. With the eyes paralyzed the two visual axes were crossed, and the fields in the right eye were to the left of those in the left eye. For each pair of cells one then asked whether the relative positions of the receptive fields in the two eyes were the same. In all of the eight simultaneous recordings the positions matched to within about 1/2°. Moreover, the directions of the deviations were more or less random, with no particular tendency for horizontal variation.

It is hard to say whether or not these variations represent departures from true correspondence, given the difficulties in comparing the two receptive-field positions precisely. For example, if one eye is strongly dominant the field in the weaker eye generally appears smaller than its counterpart in the dominant eye, since the more peripheral parts of a field often exert progressively weaker effects on the cell. Thus the possible error in determining the positions of such large fields could be of the order of 1/2°. Judging from human experience, a horizontal variation in receptive-field correspondence of up to about 1–2° would be required if such a mechanism were to be linked to binocular depth perception, but in this and other experiments one can be reasonably sure that there were no variations this great, and certainly no preferential horizontal variations. The possibility remains that there are re-
The image contains diagrams showing the differences in visual field mapping between the two eyes. The text describes how penetrations were made in both hemispheres (area 17) simultaneously, and recordings were made from cells on both sides. The two visual axes were crossed, and the fields in the right eye appear to the left, those from the left eye, to the right.

Regional specializations within 17 or 18, with variation in relative field positions in some areas and not in others. This might partly explain the discrepancy between our results and those of Bishop and Pettigrew, and of Pettigrew and Barlow; in a more extensive study of binocular correspondence of cortical cells in the cat these workers found considerable variation in relative field positions in the two eyes, both horizontal and vertical (unpublished).

**Recordings from corpus callosum**

In three experiments, seven successful penetrations were made in the corpus callosum, at Horsley-Clarke levels ranging from A2 to A6. Spikes typical of large myelinated fibers (3) were observed immediately after the electrode entered the corpus callosum, and with one or two exceptions the discharges were easily driven by visual stimulation, suggesting that this
part of the callosum is strongly preoccupied with vision. In each penetration, from 2 to 8 fibers were recorded, and in all, 34 responsive fibers were studied. Just as in cortical recordings, diffuse light was without obvious effect, but by exploring with a narrow slit of light (occasionally an edge or dark line) and constantly varying its orientation, responses were soon obtained and the receptive-field position and orientation established.

For 15 fibers an attempt was made to find out whether the field was simple or more complex. Of the 34 neurons, 7 had simple fields, with clear subdivision into excitatory and inhibitory areas; 7 were clearly complex and 1 was hypercomplex. The rest were not studied long enough for categorization. Fibers with simple fields presumably had their origin in area 17, while those with complex and hypercomplex fields could have originated from 17, 18, or 19.

For our present purposes the most interesting characteristic of these cells was the distribution of their receptive fields. Of 34 fibers, all but 2 or 3 had fields that came up to within a degree or so of the vertical meridian or overlapped it, and only 1 cell (no. 17, penetration E, Fig. 5) had a field more than 4° from the midline. Figures 4 and 5 summarize the receptive-field positions for the cells of all 7 penetrations. About half of the fields were in or very near the area centralis, and most of the others were scattered above and below it along the vertical meridian. Some indication of a crude topographic organization may be seen in Fig. 5, the cells of a given penetration tending to be mostly in the area centralis (penetration B), or all in the

**Fig. 4.** Receptive-field positions of 10 cells recorded from the corpus callosum in 2 penetrations. Histology from the second electrode track (units 8-13) is illustrated in Fig. 6.
inferior fields of vision (penetration C and E), or the superior (penetration A). It was shown histologically that all of these penetrations passed through the corpus callosum, as illustrated in Fig. 6 for one of the penetrations of Fig. 4 (cells 8–13).

All of the fibers in the corpus callosum were binocularly driven, but just as in cortical recordings there was wide variation in the relative influence of the two eyes, from fibers strongly dominated by the left eye, through equal influence, to strong right-eye dominance. As usual, the fields in the two eyes had otherwise identical characteristics, including field position, size, and orientation.

**DISCUSSION**

From the present results it seems clear that close to the 17–18 border in the cat cortex there is a bilateral representation of the vertical meridian of the visual field. Stated in terms of single cells, there are in this 17–18 border region cells whose receptive fields are not confined to the contralateral half of the visual field, but spill over into the ipsilateral half. The question immediately arises as to the connections responsible for this encroachment on the ipsilateral field. An indication that callosal connections are involved comes from the experiments in which Choudhury et al. (1) cooled the contralateral cortex or the corpus callosum, or cut the callosum while recording from the cortex on the side of the cut optic tract. Their conclusion receives support from our observations that the fibers in the posterior callosum are largely concerned with the midline.

At first glance the fact that the midline region of the visual fields is bilaterally represented in the cat cortex might seem to bear on the well-known but controversial question of macular sparing following total occipital lobe removal in man. Obviously, however, any bilateral representation which depends on projections from visual areas in the contralateral hemisphere could play no part in macular sparing attending the removal of these visual areas.

One should perhaps point out that the optic tract and lateral geniculate probably receive some ipsilateral input, and indeed it would be strange if geniculate cells with field centers along the vertical meridian were not just as plentiful as any others. These cells would have to have input from the ipsilateral half of the visual field to take care of a part of their field centers and about half of the field peripheries. The retrograde-degeneration studies of Stone (9) indeed indicate that the ganglion cell populations projecting to the two optic tracts overlap along the midline by about 0.9°.

Our results, as well as those of Choudhury et al. (1), fit well with anatomical studies which indicate that area 17 on one side projects to contralateral 18 and 19 and to the lateral bank of the suprasylvian gyrus (Clare and Bishop area; 7). We have recently found from Nauta silver-degeneration studies that 18 also has rich connections with 18 on the opposite side, but probably sends little or nothing to contralateral 17. These commissural connections by themselves would make one expect some overlap in receptive field position of
Fig. 6. Coronal section through corpus callosum at Horsley-Clarke level A5, showing microelectrode track and terminal lesion (arrow) for the penetration in which cells 8-13 of Fig. 4 were recorded. Cresyl violet stain.

cells in the two hemispheres, and indicate that one such region should be the part of 18 near the 17-18 border. The present experiments with two electrodes were too few in number to allow one to say conclusively that the region of overlap is entirely in 18. Moreover, the frequent difficulty in being certain of the exact position of the 17-18 border makes it hard to be sure

Fig. 5. Receptive-field positions of cells recorded in five penetrations in the corpus callosum. Penetration A is from one experiment, B-E from a different one. In each diagram the intersection of vertical and horizontal lines indicates the area centralis, to within a degree or so. (Field 8 of penetration D occupied the entire upper right quadrant.) The anterior-posterior position of the electrode in Horsley-Clarke coordinates is indicated for each penetration.
that the most medial strip of 17 is not also involved. This problem is likely to be less serious in the monkey, where the 17–18 border is far more precise. Taken together, the results of Choudhury et al. (1), the two experiments described here, and the anatomical studies (2, 7, 8) all indicate that a special set of connections exists for dealing with the midline representation of the visual fields. These fibers might be expected to serve the same functions as intracortical fibers linking cells with receptive fields clustered in other, more outlying parts of the visual fields. The kinds of connections required can be reasonably inferred from what is known about the single-cell physiology of 17, 18, and 19. A complex cell in 18 which overlaps the midline could, for example, receive input from simple cells, some directly from nearby 17 in the same hemisphere, and some from the opposite hemisphere via the corpus callosum. For this reason it seems interesting that the corpus callosum contains clear examples of fibers with simple receptive fields, which are not found, as far as is known, in area 18. From the fact that 17 projects to contralateral 19 on the two sides, one may similarly infer analogous connections for the elaboration in 19 of hypercomplex receptive fields which straddle the two half-visual fields.

**SUMMARY**

By recording single cells simultaneously in opposite hemispheres in the cat it was shown that the receptive fields of some cortical cells near the 17–18 boundary overlap the vertical midline of the visual fields. Overlapping was found only in the transitional zone between 17 and 18, and the adjacent part of 18. These areas are known anatomically to be interconnected, and to receive connections from the most lateral part of area 17.

Of 34 single fibers recorded from the posterior corpus callosum, all but 1 or 2 could be driven by visual stimulation, and of these all but 1 had receptive fields that overlapped the vertical midline or came up to within a degree or less of it. About half of the receptive fields were clustered around the area centralis; the rest were scattered widely above and below the horizontal meridian. Seven cells had “simple” properties, the others being complex or hypercomplex.

These results suggest that certain fibers in the corpus callosum link cells whose fields are close together but lie on opposite sides of the vertical meridian or straddle it. These fibers would therefore seem to serve the same functions as intracortical fibers linking cells with receptive fields clustered in more outlying parts of the visual fields.

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**ADDENDUM**

Since this paper was submitted, Gazzaniga, Berlucchi, and Rizzolatti have published a preliminary report on single-unit recordings in cat corpus callosum (*Federation Proc.* 26: 1864, 1967). Their main findings are in agreement with those reported here.
REFERENCES


