Combined anatomical and electrophysiological studies on the boundary between the second and third visual areas of rhesus monkey cortex

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(Communicated by J. Z. Young, F.R.S. – Received 1 July 1976)

[Plate 1]

Anatomical evidence (Cragg 1969; Zeki 1969) has shown that the horizontal meridian is represented at the boundary of the second and third visual areas of rhesus monkey cortex and that as one proceeds further anteriorly along V3 one reaches a region of V3 that is callosally connected and in which the vertical meridian is represented. We have confirmed these anatomical findings by recording from the cortex of monkeys in which the splenium of the corpus callosum had been sectioned before the recording experiments.

Introduction

It has long been known that, in the rhesus monkey, the vertical meridian is represented at the boundary of the first and second visual areas (V1–V2 boundary) (Whitteridge 1965; Cragg 1969; Zeki 1969; Hubel & Wiesel 1970). In 1969 (Cragg 1969; Zeki 1969), it was proposed on the basis of anatomical studies that the horizontal meridian is represented at the boundary of the second and third visual areas (V2–V3 boundary) and that, as one proceeds further anteriorly along V3, one reaches a region in which the vertical meridian is re-represented. Since that time, Spatz, Tigges & Tigges (1970), using anatomical techniques and Allman & Kaas (1971) using evoked potential ones, have confirmed that the horizontal meridian is indeed represented at the outer boundary of V2 (the boundary away from V1) in primates with lissencephalic brains†. But direct electrophysiological support for these anatomical results has not been available for the highly convoluted brain of the rhesus monkey. Accordingly, we decided to investigate the problem.

Although in the rhesus monkey both V2 and V3 are extensive areas representing at least 40° of the visual fields from the centre of gaze, and possibly more (unpublished results), in this study only that part of V3 lying next to V2 and representing

† Such smooth brained primates may not possess a third visual area. The nocturnal owl monkey certainly does not (Allman & Kaas 1975) and it is claimed not to exist in the squirrel monkey by Spatz et al. (1970), but this has been questioned by Cowey (1973) and Höfländer (1975).
the lower visual fields within the central 10° has been studied. This part lies in the lunate sulcus (Cragg 1969; Zeki 1969). The approach we used was to correlate anatomical results with electrical recordings in the same hemisphere. If, following section of the splenium of the corpus callosum, the distribution of fibre degeneration in the prestriate cortex is examined, several discrete patches of degeneration will be found (Zeki 1970). The first of these occurs at the V1–V2 boundary and Whitteridge (1965) has shown that this region of callosal fibre degeneration corresponds to the representation of the vertical meridian. As one proceeds down the posterior bank of the lunate sulcus (see figure 1), another region of fibre degeneration appears, either at the bottom of the sulcus or at the medial end of its anterior bank, depending upon the level of the brain examined (Zeki 1970). It has been assumed, on the basis of anatomical studies (Cragg 1969; Zeki 1969), that the region of this second patch of callosal fibre degeneration corresponds to a vertical meridian re-representation in V3. In this study we wanted to test this assumption directly by recording from the brains of monkeys in which the corpus callosum had been sectioned several days before the recording experiment. Such an approach had the added advantage that it would give information on whether in further visual areas, beyond V1 and V2, regions of midline representation are also callosally connected. In general, our expectation in these experiments was that as one records from roughly half-way down the posterior bank of the lunate sulcus, a region free of callosal connexions, cells would have receptive fields in the horizontal meridian and that this would correspond to the V2–V3 boundary. As one records more anteriorly in V3, one moves closer and closer to the second patch of callosal fibre degeneration within the lunate sulcus, and receptive fields will move closer to the midline until, at the region of the second patch of callosal fibre degeneration, cells will have receptive fields at, or extending to, the midline. Both these expectations were realized.

**Methods**

The surgical, electrophysiological and histological procedures have been described elsewhere (Zeki 1970, 1974). The corpus callosum was sectioned six days before the recording experiments, a survival time which allows callosal fibre degeneration to show up optimally (Zeki 1970).

In these experiments, which are concerned with the topographic representation of the visual fields in the cortex, an accurate determination of eye position was critical. We therefore plotted the position of the fovea on the tangent screen, using a reversible opthalmoscope, before and after every receptive field plot. As an additional precaution, we used the reference cell technique of Hubel & Wiesel (1973). A binocularly driven, colour coded cell in the fourth visual complex (Zeki 1973) of the opposite hemisphere was isolated with a second, reference, micro-electrode and its receptive field was replotted regularly during the experiment. By using both these checks, drifts in eye position could be easily detected and corrected.
The animals were anaesthetized with sodium pentobarbitone and paralysed with Flaxedil, repeated doses of the anaesthetic being given during the course of the experiment to maintain adequate levels of anaesthesia (Zeki 1974). End tidal CO$_2$ was measured on a Beckman LB 1 gas analyser and maintained at between 3–4 %. Recordings were made from groups of cells with low impedance (15–20 μm exposed tip) tungsten-in-glass microelectrodes. To identify the position of the recording sites, one or more lesions were made in some of the penetrations by passing a d.c. current (7 μA for 7 s) through the microelectrode (tip negative). At the end of the recording experiments, the animals were perfused and the brains sectioned and stained according to techniques already described (Zeki 1970).

Results

Figure 1 illustrates an experiment in which five parallel penetrations were made, using the same microelectrode, through the lunate sulcus of an animal in which the corpus callosum had been sectioned six days before the recording experiment (see also figures 5 and 6, plate 1). In penetration A, which was the most medial, cells were sampled in both the posterior and anterior banks of the lunate sulcus. The first two groups of cells had receptive fields clearly away from the midline. The third and fourth groups of cells recorded from in this penetration had receptive fields on the horizontal meridian. In the remaining four penetrations, cells were sampled in the anterior bank of the lunate sulcus only. Although there was a certain amount of receptive field scatter, the results of the five penetrations are unambiguous – as one moves closer to the second patch of callosal fibre degeneration in the lunate sulcus, so cells have receptive fields closer to the midline, until, at the region of the second patch of callosal degeneration (figure 1, track E), cells have receptive fields at the midline. An alternative manner of showing this change in visual field representation is illustrated in figure 2. In this figure, based on the same experiment as that of figure 1, all the receptive fields in the five tracks have been plotted but five of these have been drawn in heavy lines. These five receptive fields are those of cells in the five positions marked on the section drawing of the brain and show quite clearly that as one moves from the bottom of the lunate sulcus to the region of the second patch of callosal fibre degeneration, so receptive fields move from the horizontal to the vertical meridian. It is interesting to note that in this progression receptive fields invade the superior quadrants of the visual hemifields (see figures 1 and 2).

It has also been suggested (Cragg 1969; Zeki 1969) that as one moves dorsally in the lunate sulcus, so receptive fields in this part of V3 move inferiorly – that is to say that V3 is topographically organized in the dorsoventral axis as well as in the antero-posterior axis. This was tested in the experiment illustrated in figure 3. In this animal, two parallel penetrations were made in the anterior bank of the lunate sulcus, just medial to the second patch of callosal fibre degeneration, at a level of the sulcus more dorsal than the ones illustrated in figure 1. As expected,
Figure 1. Reconstruction of five parallel penetrations through the lunate sulcus of an animal in which the corpus callosum had been sectioned six days before recording. The dots in the cortex represent the degeneration following callosal section. The penetrations were made at the level indicated on the drawing of the brain to the lower left. Positions of entry of the electrodes is marked by an X. The short horizontal lines meeting the long common electrode tracks indicate the position of the cell groups recorded from, and these are numbered in each track. Circles represent positions at which lesions were made. The receptive field of each group of cells in tracks A–E is plotted as a rectangle or a square, since all the groups encountered in these penetrations were orientation selective. The receptive fields of cells in each track are separately indicated in the plots A–E. Note the position of group 4 in track A and the gradual move towards the midline from A to E. Track E was in a region of callosal degeneration and the cells of this track had receptive field at the midline. Continuous line in the cortex represents V1. See also plate 1.

Description of Plate 1

Figure 5. Low power photomicrograph, taken in dark field illumination, to illustrate the five parallel penetrations through the lunate sulcus shown in figure 1. All five tracks are identifiable in this one section, as are some of the lesions. The region between the arrows is the area of degeneration in the lunate sulcus and degenerating fibres can be seen as fine white dots. I.e., lunate sulcus.

Figure 6. Photomicrograph to show a lesion and the degeneration in the same section. The lesion shown here belonged to that made in track E of the experiment illustrated in figure 1 and shown in figure 5 above.
Figures 5 and 6. For description see opposite.
cells had more inferiorly situated receptive fields. Both penetrations were clear of the second patch of callosal degeneration and in both penetrations cells had receptive fields clear of the midline. Note that cells in the more medial of the two penetrations had receptive fields further away from the midline than cells encountered in the more lateral penetration.

**Discussion**

Our conclusions from these combined anatomical and electrophysiological experiments may be summarized as follows: (1) As one moves medially in the posterior bank of the lunate sulcus from the vertical meridian representation at the V1–V2 boundary, so receptive fields move out towards the horizontal meridian. (2) As one moves closer to the second patch of callosal fibre degeneration in the anterior bank of the lunate sulcus, receptive fields move closer to the midline. (3) At the second patch of callosal fibre degeneration, cells have receptive fields at the midline. (4) Callosal connections in regions of the prestriate visual cortex beyond V2 are indicative of midline representation of the visual fields. As is described in detail elsewhere (Zeki 1970) and indicated in figures 1, 2 and 3, there are further discrete regions of the prestriate cortex, beyond that part of V3 studied.
here, which also have callosal connections. The approach used in this study, of combining anatomical and electrophysiological studies in the same animal, provides, therefore, a powerful tool for defining these further areas of the prestriate visual cortex (see also Zeki 1976).

It should also be pointed out that cells have much larger receptive fields in V3 than in V1 (Hubel & Wiesel 1968) or in V2 (Zeki, unpublished results) and that there is a difference in magnification factors between these areas. Magnification factors (Daniel & Whitteridge 1961) refer to millimetres of cortex per degree of visual field at different eccentricities. Reference to figure 1 will show that it takes

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**Figure 3.** Reconstruction of an experiment in which two parallel penetrations were made through the lunate sulcus at a level indicated on the surface drawing of the brain to the left. The splenium of the corpus callosum had been sectioned six days before the recording experiment. Conventions as in figure 1. Note (a) that in these penetrations, which were made at a more dorsal level to those shown in figure 1, cells had receptive fields more inferior in position in the visual fields and (b) that both tracks were clear of the patch of callosal degeneration and that the cells had receptive fields clear of the midline (except for two in the more lateral track whose very edges only reached the midline).
3 mm to get from 5° out on the horizontal meridian (track A, group 4) to the vertical meridian in this part of V3 (track E) whereas it takes over 12 mm to get to the vertical meridian representation at the V1–V2 boundary (see figure 1). In V1, at comparable eccentricities, 6 mm of cortex is devoted to the central 1° of the visual fields (Daniel & Whitteridge 1961). We conclude that, since V3 receives a direct input from V1 (Cragg 1969, Zeki 1969), this input must be a convergent one.

The results given in this study, as well as antecedent anatomical ones and unpublished results, allow us to draw a more definite boundary between V2 and V3 (see figure 4). Although this boundary may vary slightly from one level of the lunate sulcus to another, as drawn it is as accurate as we are likely to get it by electro-physiological methods at the present time. It is at this boundary that a point 5°–7° out on the horizontal meridian, and apparently a turning point, is represented and movement away from this boundary in either direction leads increasingly towards the vertical meridian (although it takes longer, in terms of distance travelled, to reach the vertical meridian representation in V2 than that in V3 (see figure 4)). Although we have only studied a limited portion of V3 with this technique so far, V3 itself continues as a belt around V2, extending into the more dorsal part of the lunate sulcus and then into the parieto-occipital sulcus. More peripheral parts of the visual fields are represented in these, more distal, parts of V3 but we have no reason to believe that the general organization of V3 and its
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relation to V2 are in any way different to what we have described for the more central parts of V3.

It is, finally, very gratifying to learn from these results that interpretations based on the relatively crude lesion technique have been borne out in all essential details by the more accurate methods used here.

This work was supported by the Science Research Council.

We are greatly indebted to Ms Brenda Crane and Ms Pamela Jacobs for their excellent histological assistance.

We would like to record our thanks to Professor J. Z. Young, F.R.S., and Professor Sir Bernard Katz, Sec. R.S., for their critical reading of this manuscript.

REFERENCES


Cragg, B. G. 1969 The topography of the afferent projections in the circumstriate visual cortex (C.V.C.) of the monkey studied by the Nauta method. Vision Res. 9, 733–747.


Figures 5 and 6. For description see opposite.