The nature of the boundary between cortical visual areas II and III in the cat

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The representation of the visual field in the second and third visual cortical areas (V II and V III) of the cat was examined by microelectrode recording. The position of the field maps and the arrangement of the map within V II were found to vary greatly from one cat to another so that no single composite map can be made. The horizontal meridian of the visual field was found to run laterally and forward from V I across V II to V III. The reversal of field sequence, which indicates the V II/V III boundary, was very variable both from cat to cat and in the same cat for points above and below the horizontal meridian. The commonest situation was one in which the reversal point was 40° for some lines of latitude, but for others the reversal point was only 6–15° out. This means an ‘island’ of representation of points 40° out was bounded by areas of representation much closer to the vertical meridian. In some cats one ‘island’ was plotted, in one there were two completely plotted and in others there were two ‘islands’, one complete, one incompletely plotted. In one cat no ‘island’ was found, and the boundary between V II and V III seemed to be formed anteriorly and posteriorly by the vertical (longitudinal) meridian 20° out. The islands contain many units with markedly elongated receptive fields whose particular function is not yet clear. The arrangement of the V II/V III boundary found in these experiments is compared to that previously suggested and to present knowledge of the mapping in primate visual cortex.

Introduction

The striate cortex (visual I) in the cat is known to contain a topographic representation of the whole contralateral visual field (i.e. to at least 90° lateral) and to correspond to cytoarchitectonic area 17 of Otsuka & Hassler (1962) (Hubel & Wiesel 1965; Whitteridge 1973; Kalia & Whitteridge 1973). The lower field is expanded at the expense of the upper field (Bilge, Bingle, Seneviratne & Whitteridge 1967). A visual area lateral to the striate cortex was described by Talbot (1942) and illustrated by Woolsey & Fairman (1946) who named it visual II. Talbot believed that only a region near the vertical meridian was represented there.

It is now apparent that visual II does not contain a map of the whole contralateral field (Hubel & Wiesel 1965; Woolsey 1971; Whitteridge 1973; Tusa,
Palmer & Rosenquist 1975; Tusa 1974) and that there is no representation of receptive field centres beyond about 40° lateral to the vertical meridian. The map is arranged as a mirror image of visual I and the visual I/II boundary is the vertical meridian. Visual II corresponds closely to cytoarchitectonic area 18. Hubel & Wiesel (1965) found that in some experiments the visual II map extended to only 15° though in others it reached 40° and suggested that, at some anteroposterior cortical levels, there is no representation of the peripheral field, and Woolsey (1971) reached a similar conclusion.

Visual III was described by Hubel & Wiesel (1965) as an area lateral to visual II containing a map reversed with respect to V II, that is, the same way round as visual I. They did not map it completely but it seemed to coincide with area 19 of Otsuka & Hassler. Woolsey (1971) denied that there was a reversal of the direction of progression of field centres as the recording electrode passed lateral to V II. Bilge et al. (1967) and Whitteridge (1973), however, confirmed the reversal reported by Hubel & Wiesel (1965) and concluded that the boundary between V II and V III is related to the representation of the horizontal meridian, though the later experiments (Whitteridge 1973), seemed to indicate that the horizontal meridian divided to separate upper and lower field representations in visual II and III into pairs. In 1974 Tusa denied that the 18/19 border is formed by the horizontal meridian but, later, Tusa (1975) concluded that it separates upper field representations in V II and V III but that lower field representations are divided by the representation of the ‘outer lower visual periphery’. Allman & Kass (1975) and Tusa et al. (1975) have recently reported multiple representations of the visual field in the extra-striate cortex of the owl monkey and of the cat (the details differ in the two species). We noticed, during experiments on visual II, that the mapping seemed very variable in respect of how much periphery was represented. We therefore carried out a series of mapping experiments on V II and its boundaries and also re-examined maps from two earlier experiments in which a particularly large area of cortex had been studied, in an attempt to form a clear picture of the nature of the map in V II and of its relation to the horizontal and vertical meridians.

A preliminary report of some of the results has appeared (Donaldson, Kalia, Nash & Whitteridge 1976).

Methods

The visual cortex of the left hemisphere of 15 cats was studied. In the first three experiments anaesthesia was induced with sodium pentobarbitone (Nembutal) 30 mg/kg intramuscularly and maintained with intermittent intravenous doses of pentobarbitone. In two experiments induction was with halothane (Fluothane) and, in the remaining 8, a steroid anaesthetic, Althesin (Glaxo), 18 mg/kg intramuscularly was used, followed by chloralose 70 mg/kg intravenously when the inducing anaesthetic had almost worn off.
When arterial, venous and tracheal cannulae were in place, the cervical sympa­thetic trunk was cut bilaterally to reduce to a minimum residual eye movements (Rodieck, Pettigrew, Bishop & Nikara 1967) and the head was fixed in a stereotaxic head holder which left the visual fields unobstructed. The eyes were treated with phenylephrine (10% in 0.9% saline) and atropine (1%) to retract the nictitating membranes and dilate the pupils, and neutral contact lenses were applied. A craniotomy was made over the left cerebral cortex from about 4 mm anterior to 4 mm posterior to the interaural plane and extending mediolaterally from just right of the midline to beyond the left lateral sulcus. The dura mater was reflected and the cortex was covered with warm Agar (2½% in 0.9% saline) to a depth of at least 1 cm. When this had hardened, it satisfactorily controlled cortical pulsation. The animal was then paralysed with gallamine (Flaxedil) and a slow intravenous infusion of gallamine (56 mg/h) was started which maintained paralysis for the rest of the experiment. Artificial ventilation was with either air, air enriched with oxygen or a mixture of N₂O (70%) with O₂ (30%). The expired CO₂ was measured with an infrared analyser and the minute volume was adjusted to keep the end-tidal CO₂ between 4% and 5%. Body temperature was kept about 38°C by a thermostatic blanket and the arterial pressure was monitored.

Recording

Tungsten microelectrodes sharpened electrolytically and insulated with Bakelite varnish were used in early experiments; later, glass-coated tungsten electrodes (made by the method of Merrill & Ainsworth (1972) but unplated) with exposed tips of about 15 μm (impedance 1–2 MΩ at 1 kHz) were found to give much more satisfactory records though their greater flexibility often made it difficult to penetrate the cortex at the desired angle.

Two approaches were made for mapping. Either a series of vertical electrode penetrations was made spaced 0.5–1 mm apart along medio-lateral rows or the electrode was introduced at about 30° to the horizontal near the medial edge of the left hemisphere and driven laterally so that it passed approximately parallel to the surface of the lateral gyrus. Each approach had its peculiar advantages and disadvantages (see below). The ends of recording tracks were marked by electrolytic lesions (about 6 μA for 15 s, electrode tip cathode). Receptive fields of single units were plotted on a target screen 114 cm from the eyes each time the electrode had advanced by about 100 μm in the later experiments or by 500 μm in the two early ones. Stimuli were hand-moved bars and edges. The positions of the optic discs were plotted on the Perspex tangent screen by using an indirect ophthalmoscope (see Clarke & Whitteridge 1976) and were checked at intervals during the experiments. From the position of the optic disks the field positions were related to a system of ‘spherical polar coordinates with the axis vertical’ and passing through the estimated vertical meridian (Bishop, Kozak & Vakkur 1962; Joshua & Bishop
The estimate of the vertical meridian was corrected by reducing to zero the average separation of the members of receptive field centres of binocular units in area 17 and the position of the horizontal meridian was taken as $7.5^\circ$ below the horizontal line bisecting the vertical interval (if any) between the optic disk centres (see Nikara, Bishop & Pettigrew 1968, and Discussion in present paper).

**Histology**

At the end of all experiments the brain was perfused with 0.9% saline followed by neutral buffered formalin via the aorta. The calvarium was later removed and the head in its holder replaced on the stereotaxic machine and a block of brain cut with its faces parallel to the rows of electrode tracks. In some experiments a pair of marker holes was made normal to the cut surface to give reference points for aligning the sections during reconstruction. After further fixation the brain was frozen or embedded in celloidin and sectioned at 50 $\mu$m parallel to the electrode tracks and stained for Nissl material. Sometimes alternate sections were stained by the Weil method for fibres. Electrode tracks were reconstructed on tracings of sections enlarged 20 or 30 diameters and recording sites were marked on these allowing for shrinkage during histological preparation, calculated, for each reconstruction, from the track separation or the position of lesions. Maps of the representation of the visual field were constructed from measurements of the positions of the recording sites and projected on to a ‘flattened out’ cortical surface. Deep recording sites were projected to the intersection with the cortical surface of a line normal to the surface and passing through the recording site.

**Results**

We found that there is a great deal of variation in the arrangement of the map of the contralateral visual field in V1 from one cat to another. As will appear, it is not possible to make a composite map by using the results of several experiments. This leads to two difficulties. It is impossible to choose a particular region of the field whose map is of interest and have any certainty of finding its representation in a given experiment: instead it is necessary to map as large an area as possible for each cat, and inevitably it turns out that interesting regions remain unmapped in many experiments. It also means that we have to describe individual experiments chosen to illustrate the various types of map which we have encountered. The variability of the position of the boundaries of the visual maps was described briefly by Whitteridge (1973). As well as the variations in sulcal arrangement on the dorsal surface of the hemispheres described by Otsuka & Hassler (1962) we have noticed that there is a good deal of variation between cats in the extent to which the posterior wall of the spenial sulcus is folded in where the sulcus runs laterally and downwards. Increased infolding of this sulcus would be expected to result in displacement of the visual cortex posteriorly and medially.
As an example from the present experiments, the cortex at the anteroposterior level of the interaural plane (i.a.p.) represented the horizontal meridian in one experiment (figure 1a) but in the others units on the i.a.p. had field positions from 3° to more than 10° below the horizontal.

**Representation of the horizontal meridian**

The representation of the horizontal meridian appears to run laterally and slightly forwards across the cortex traversing visual areas i, ii and iii. Our observations confirm once again that the representation in V ii is arranged in mirror-image order compared to V i, and that of V iii is in turn a mirror image of V ii. The sequence of progression is illustrated by figure 1a and b. The horizontal row of points at 1 mm anterior to i.a.p. in (a) is reconstructed from the six electrode tracks shown in (b) and represents field positions within 1° vertically of the horizontal meridian. Track 1 is in area 17 by the criteria of Otsuka & Hassler (1962) and track 2 is on, or very near, the cytoarchitectonic estimate of the 17/18 border. Field positions in these tracks lie within 1.5° of the estimate of the vertical meridian; two fields appear to lie a little way into the ipsilateral hemifield. Tracks 3, 4, 5 and 6 are in the medial wall, base, and lateral wall, respectively, of the lateral sulcus. The field positions move out to 15° at the lower end of track 4 then progressively to 39° as one ascends track 5. However, the field centres do not then go any further laterally but reverse their progression to move towards the vertical meridian and reach 19° at the top of track 5 and 12° in track 6. The reversal at 39° marks the boundary between visual ii and visual iii. The transition from area 18 to area 19 on cytoarchitectonic criteria falls in the region of the 39° representation. It is clear from figure 1b that there is no region of unexplored cortex between the furthest lateral representation (39°) and the fields more medial in V ii (lower on track) or in V iii (above 39° on track) in which any more peripheral field-representation could lie since the reversal occurs on a single, continuously explored, electrode track. If there were any representation of the field beyond 39° it would, presumably, lie between the 39° observations. We cannot exclude the possibility that one of our 100 µm electrode advances entirely ‘skipped over’ such a representation, which would have to be totally contained in 100 µm of cortex and would thus have a very much smaller magnification factor than that for the peripheral field in visual i.

Figure 2a, b, shows the representation of part of the horizontal meridian in another cat, 1 mm posterior to i.a.p. The lateral two tracks of figure 2b, lying in the medial wall of the lateral sulcus, contain a representation of field centres out to 42° and back to 9° at the bottom of the lateral sulcus. Comparison of these two experiments shows that in each case the progression of the receptive fields is the same but in the experiment of figure 2 the V ii/V iii boundary lies in the medial wall of the lateral sulcus while in that of figure 1 it is in the lateral wall of the sulcus. Probably this is related to the presence of a suprasplenial sulcus (su.s.) in figure 2b and c and its absence in figure 1b.
The map from a third experiment (figure 3) shows another example of representation of field centres out to 46° on the horizontal meridian with subsequent reversal of the direction of progression as the recording sites are situated more laterally.

**Figure 1.** For description see opposite.
The representation of the upper and lower fields in visual II and visual III

In V II as in V I the lower field is represented anterior and the upper field posterior to the representation of the horizontal meridian, as has been reported by others (Hubel & Wiesel 1965; Bilge et al. 1967; Tusa 1974; Woolsey 1971). The present experiments give information largely on the lower field whose representation occupies more cortex than that of the upper field (Bilge et al. 1967). No representation was found of field centres beyond 46°. However, there seemed to be very pronounced differences between cats in the arrangement of areas of field away from the horizontal meridian. The contour map of figure 3 shows that in this cat there was representation out to 40° on the horizontal meridian with a regular decline in the most lateral representation to 30° then 20° as one moved anteromedially or posterolaterally on the cortex. The 10° contour is complete anteriorly but the map does not extend far enough posteriorly to show whether it closes in the upper field. Thus, in this cat there was a single ‘island’ of 40° representation surrounded by regions of progressively more restricted representation both anterior and posterior to the representation of the horizontal meridian.

Figure 2a shows our best example of a representation with two ‘islands’ each reaching 40°. The posterior island (row at posterior 1 mm on figure 2a) sits astride the representation of the horizontal meridian as described above; it has complete contours for 40°, 30° and 20°. Between 1 and 4 mm anterior to i.a.p. lies a second island in which a representation of field centres up to 40° out at about 15° below horizontal is found; it also has complete 40°, 30° and 20° contours.

Between these islands there is a ‘channel’ in which the most lateral field centre is only 17° out. Figure 2c shows the four electrode tracks from which this row of the map, on i.a.p., was constructed. It shows a reversal of field progression at 17° in the medial wall of the lateral sulcus. The cortex in the depth of the sulcus was not mapped but the sequence of field positions makes it very unlikely that the unmapped cortex of the lateral wall of the sulcus could contain a representation.
Figure 2. For description see opposite.
beyond 17°, indeed this would require an additional pair of reversals of the progression. Thus the V II/V III boundary in this case is at 17° and is found at about the same level in the wall of the sulcus as the 42° representation which forms the boundary 1 mm posterior to i.a.p. (figure 2b). This pair of reconstructions is an example of the evidence that the posterior 40° island is bounded by a region which contains the V II/V III boundary and in which the furthest field centre is less than 20° from the vertical meridian. Indeed, in this experiment the six reversals of progression which were found over the five millimetres between P3 and A2 all occurred in the medial wall of the lateral sulcus, the site of reversal gradually rising as one passed forward to reach the surface of the gyrus in A2. This regular progression would correspond to the positions of the cytoarchitectonic 18/19 boundary at these levels. Any representation of the field further out than that recorded for the reversal would have to be contained in about 1 mm of cortex in this (early) experiment for it to have been missed. That there is no technical difficulty in detecting representations of the peripheral field to well beyond 40° is

**Figure 3.** Map of part of visual II and III in the left hemisphere of a cat in which a single ‘island’ of representation of the periphery up to 46° was found. Conventions as for figure 1a. The horizontal meridian is represented at P5 and a part of the upper field is mapped (bottom two rows of points in the figure).

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**Figure 2.** (a) Map of part of visual II and III in a cat in which two ‘islands’ of representation of the periphery up to 40° were found. Conventions as for figure 1a. (b) Section showing the tracks from which the row of figure 2a at P1 was constructed. The representation is of the region on and near the horizontal meridian; (su.s.) suprasplenial sulcus. Conventions otherwise as for figure 1b. (c) Section showing the tracks for the row on the i.a.p. in figure 2a. Conventions as for figure 2b.
Figure 4. For description see opposite.
shown by the results of Kalia & Whitteridge (1973) on the splenial cortex, which include fields up to 90° out.

The experiment of figure 1 discussed above shows what appears to be the major part of a single island bounded anteriorly by a region in which the representation reaches only 12°. We do not know whether this cat had further islands more posteriorly.

Figure 4a shows a map of an experiment in which the lower field from 8° to about 16° below the horizontal meridian was mapped, and the section (figure 4b) shows the single tangential electrode track on which the map row at anterior 1.3 mm is based. After the first three field centres (right of figure 4b) which appear to lie in the ipsilateral hemifield, there is a sequence out to 25° with reversal from there to reach 11° at the end of the track. There is no unexplored cortex along the track. In this cat, at 1.3 mm anterior to i.a.p. the \( V_{\text{II}}/V_{\text{III}} \) boundary lies on the exposed surface of the lateral gyrus and occurs at 25° in the field. Thus the island reaches only 25° at its centre. Note that this cat has a wide and shallow lateral sulcus at this level.

In contrast, the map of a similar region of the lower field (7° to 10° below horizontal) in figure 5 shows no evidence of an island. The reversals and thus the \( V_{\text{II}}/V_{\text{III}} \) boundary occur at 17° in the row at P2 and 14° at P3. Although a similar region of the lower field is represented by this map it lies at least 3 mm more posteriorly on the cortex than that of figure 4, with the i.a.p. as reference.

Finally, figure 6a shows a map which appears to contain two islands, though neither is completely defined, which reach only 14° at the reversal and which are separated by a region where reversal occurs at 6°. The row at P2 is probably close to the representation of the horizontal meridian. The sections showing the tangential electrode tracks at A1 and A2 (figure 6b and c) show clearly the sequence reversals and that there is no unmapped cortex in the region of reversal in which more peripheral field positions could be represented. In figure 6c the 18/19 border determined cytoarchitectonically is marked. The coincidence of the 18/19 boundary region and the sequence reversal is clear.

None of our experiments provides a complete map of visual area III. We have evidence of representation of the contralateral hemifield to within 1° of the vertical meridian, at least near the horizontal meridian, and can confirm that the magnification factor in the central representation is considerably greater than for the peripheral field.

**Figure 4.** (a) Map of part of visual II and III in the left hemisphere of a cat with an 'island' of representation which reached only 25° lateral. The dotted line crossing the island vertically is the position of the \( V_{\text{II}}/V_{\text{III}} \) border (\( V_{\text{II}} \) to the right of the figure). Conventions as for figure 1a. (b) Drawing of a section of the brain of figure 4a showing a single electrode track approximately parallel to the cortex of the lateral gyrus at A1.3 and showing the recording sites for the uppermost row of figure 4a. Negative values are in ipsilateral field (see text). The end of the track is marked by a lesion; (l.s.) lateral sulcus, (s.s.) splenial sulcus.
Properties of the fields in \( V_{II} \) and \( V_{III} \)

It was clear that, as in \( V_I \), the field size increases in general as the field centres move peripherally. Fields with centres between 10° and 20° out were often strikingly elongated with a horizontal measurement several times the vertical. The maximum horizontal to vertical \((H/V)\) ratio was 5.8 but more commonly \(H/V\) was between 2 and 3 at this eccentricity. Fields with centres between 20 and 30°

also tended to be elongated horizontally but the field width was in general smaller and the \(H/V\) ratio did not exceed 1.9. These fields almost always had as preferred stimulus a straight edge oriented approximately horizontally, that is, parallel to their long axis, and moved vertically. They did not exhibit hypercomplex properties (see Hubel & Wiesel 1965) even when they were encountered in a sequence returning to the vertical meridian and thus belonged to units in \( V_{III} \).

**Figure 5.** Map of part of visual \( V_{II} \) and \( V_{III} \) in a cat in which no 'islands' were found. The \( V_{II}/V_{III} \) boundary is at about 17° out at \( P_2 \) and 14° out at \( P_3 \). Conventions as for figure 1a.

**Figure 6** (a) Map of part of visual \( V_{II} \) and \( V_{III} \) in the left hemisphere of a cat. There are two 'islands', incompletely mapped, reaching only 14° in the contralateral field. The horizontal meridian is probably represented by the lowest row but has not been mapped out to the \( V_{II}/V_{III} \) boundary. Conventions as for figure 1a. (b) Drawing of a section showing the single recording track for the row \( A_1 \) in figure 6a. Conventions as for figure 4b. (c) The recording track for the row at \( A_2 \) in figure 6a. 18/19 position of the boundary between area 18 and 19 determined by cytoarchitectonics. (l.s.) lateral sulcus, (s.u.s.) supraasplenial sulcus, (s.s.) splenial sulcus, (H) one of two horizontal reference tracks.
Visual II/III boundary in the cat

Figure 6. For description see opposite.
In some of these units the fields extended from quite close to the vertical meridian to 20° or more out. More laterally we found fields within 5° of the vertical meridian which were small and had hypercomplex or even higher order hypercomplex properties. Many were binocular and of these some could not be driven by either eye alone. The most nearly complete map of V iii in these experiments is seen in figure 2a, but its extent and the properties of cells near the lateral border of V iii and at the V ii/V iii border have been confirmed in other experiments which covered parts of V iii.

**DISCUSSION**

**Reliability of the maps**

A considerable problem is posed by the variability from one cat to another of the position of the representation of a given part of the field on the cortex and of the details of the representation. This means that one cannot prepare a composite map which would be useful in planning experiments but is forced to make a series of observations on each individual cortex and use the sequence of field positions to deduce one’s position on the map. Even then, it is very difficult to examine large enough areas of cortex to obtain a detailed map because of the very large number of time-consuming operations required. Thus we cannot be certain that those animals which appeared to have no ‘islands’ of peripheral representation did not have such an ‘island’ in the unexplored region. In all our electrode tracks which crossed the 18/19 border we failed to observe any receptive fields centred between 45° and 85° out. In figure 1b, where there was 400 μm between observations at the reversal point, this distance would have had to contain 40° + 40°, which gives a magnification factor of 0.005 mm per degree. In other cases where the interval between observations was smaller, magnification factors of about 0.001 would have been required. It follows that if we missed the field peripheral to 45°, it must have had a magnification factor between one tenth and one fiftieth of that for corresponding parts of V1 (Kalia & Whitteridge 1973).

We found that recording along tracks approximately parallel to the cortical surface gives excellent sampling of activity in the exposed gyrus (figures 4b, 6b, c). However, it is clearly of little use in exploring the walls of sulci when vertical tracks have clear advantages (figures 1b, 2b, c).

We have relied on the projections of the optic disks, and the average relations of the meridians to these, described by Nikara *et al.* (1968) to estimate the approximate positions of the meridians. For the vertical meridian the estimate was corrected by using the average separation of the pairs of fields of binocular units in area 17. Some uncertainty remains but this is unlikely to exceed about 1° in the estimate of the vertical meridian (see Nikara *et al.* 1968). Thus it seems unlikely that those field centres which appear to lie a few degrees into the ipsilateral field have been displaced from the contralateral hemifield by errors in the estimate of the vertical meridian, and likely that these fields do extend into the ipsilateral
hemifield. For the horizontal meridian no correction is available and we have used the average value (7.5° below the optic disk) of Nikara et al. (1968). Although comparison of the absolute coordinates from cat to cat may be disturbed by these errors they are not important within a single map, nor could they produce the obvious differences in arrangement from one cat to another.

The representation of the horizontal meridian and the V II/V III boundary

In all the experiments in which it was mapped the horizontal meridian ran more or less transversely across visual areas I, II and III.

Although all are agreed that the vertical meridian divides V I from V II there is no unanimity about the nature of the V II/V III boundary. Hubel & Wiesel (1965) who first described a visual map lateral to area 18 of the cat imply that the V II/V III boundary is found at the most peripheral field representation. Woolsey (1971) denied that there is a reversal of progression of field sequence at the lateral edge of V II (see below). Bilge et al. (1967) suggested that the horizontal meridian divided V II from V III laterally but that the upper and lower field representations were separated by an area opposite the representation of the area centralis. Later, Whitteridge (1973) suggested that the upper and lower field representations in V II and V III were separated into pairs by the two arms of a split horizontal meridian in such a way that, near the representation of the area centralis, one could pass from V I into V III without crossing V II. In 1974 Tusa said that in the lower field the periphery was represented ‘laterally, along the 18/19 border’ but in 1975, Tusa et al. added that the border between the upper field representations in V II and V III is formed by the representation of the horizontal meridian. This would seem to require a dislocation of the upper field representation in V III and perhaps V II. Unfortunately, at the time of writing, Tusa’s results have only appeared in summary form.

The present experiments show the horizontal meridian progressing across V II and V III without much deviation at the border. We found that, in a favourable experiment (see figure 1a) the fields moved out in sequence along the horizontal meridian, reversed at about 40° out (defining the V II/V III boundary) and returned towards the vertical meridian along a similar trajectory. This would seem to be conclusive evidence that the boundary is formed by the 40° representation and not by the horizontal meridian. The same arrangement was found anterior on the cortex (lower field) whether an ‘island’ or a ‘channel’ was being mapped; in either case the reversal occurred at the most lateral representation and without the horizontal meridian being crossed. These observations are consistent with Tusa’s results of 1974. For the upper field we have less information, but in our maps there does not appear to be any evidence that the reversal of progression of fields is associated with a deviation towards, even less with a reversal on, the horizontal meridian. We suggest that the upper field arrangement is similar to that for the lower field, with the V II/V III boundary formed by the peripheral representation, though it occupies a smaller area of cortex and an area difficult to explore and
reconstruct because of the steep curvature of the posterior pole of the hemisphere and the infolding of the postlateral and splenial sulci.

The cytoarchitectonic boundary between areas 18 and 19 was plotted only in those experiments in which the histological evidence was adequate. We agree that the disappearance of large pyramidal cells in layer III (Otsuka & Hassler 1962) at the edge of area 18 is the most useful criterion for its detection. The reversal of field sequence appeared to correspond very well with the transition from area 18 to area 19, confirming the conclusions of Hubel & Wiesel (1965).

The failure of Woolsey (1971) to find a reversal at the 18/19 boundary was probably due to lack of exploration of the walls of the lateral sulcus, the use of evoked potentials and a macroelectrode as well as the impossibility (as it now appears) of using a standard map to predict where this boundary would occur in a given cat.

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The extent and arrangement of the map in V II

Hubel & Wiesel (1965) found that in some experiments the lateral boundary of V II occurred at only about 15° whereas in others the lateral edges of the (very large) receptive fields reached 60° and suggested that, at some anteroposterior levels, the peripheral field is unrepresented, as if the large representation of the area centralis 'had crowded the lateral representations into more anterior and posterior parts of the cortex'. Woolsey (1971) made similar suggestions.

The present experiments would indicate a rather different arrangement. It seems that, along the horizontal meridian, there is usually representation of field centres to about 40° out: this is, of course, roughly opposite the representation of the area centralis in V II and V I. More anteriorly and posteriorly however there seems to be a great deal of variation between cats. There may be one, or possibly more, 'islands' of representation in which part of the peripheral lower field is represented as far as 40° (see figures 1a, 2a, 3) or only to 25° (figure 4a) or even 15° (figure 6a). Between these islands the representation extends less far, sometimes to only 6° lateral (figure 6a). Thus, the boundary between V II and V III which we believe is defined at each anteroposterior level by the most lateral field representation in V II and which lies roughly parallel to the V I/V II boundary on the cortex; would, when drawn on a map of the visual fields, pursue a very wavy course. Sometimes the curves are very steep and reliable interpretation is very difficult when the electrode may be running parallel to, then suddenly crossing, these steep contours. Nevertheless, the close spacing of contours in some parts of the map is well supported by our results. We have found changes of over 20° in the field, per millimetre of cortex, and these were continuous, that is, there was a continuous progression of field centres over the millimetre. For example, in track 5 of figure 1b there are changes from 14° to 34° then from 39° to 19°, each occurring progressively over about one millimetre of cortex. The continuity of the change in field position over these short lengths of cortex is detectable only when the field positions are plotted at small increments of electrode position (about 100 μm in our later experi-
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ments). We feel that one must be sceptical of claims of discontinuity of field representation in the cortex unless the relevant cortical interval has been covered with very closely spaced recording steps.

The dorsal lateral geniculate nucleus (l.g.n.) sends a direct projection to area 18 in the cat (Garey & Powell 1967; Glickstein, King, Miller & Berkley 1967). If the lateral field in V II is represented only in islands, the projections from the most lateral part of the l.g.n. (in which the peripheral field is represented; see Seneviratne & Whitteridge 1962), would be expected to run to discrete patches of area 18. This does seem to be the case according to Rosenquist, Edwards & Palmer (1974) who injected radioaminoacid into the most lateral part of the l.g.n. and found silver grains in two discrete patches in area 18 at rostral and caudal levels, but not in intermediate sections (cf. their fig. 4). This would correspond well with our map of the cat with two 40° islands (figure 2a). Callosal fibres would not be expected to connect the islands and the results of Ebner & Myers (1965) indeed show no callosal connections of these parts of area 18.

It would be reasonable to suppose that the islands of peripheral representation might contain groups of units with some particular functional specialization. The only distinguishing property which we found was the common occurrence in the islands of units with long narrow fields preferring horizontal edges moved vertically. In general, although some were binocular, they did not show any striking binocular interaction in their responses and they would seem quite inappropriate as part of a mechanism of stereopsis. They might be of use in detecting the direction of horizontals such as the horizon relative to the head. It is interesting that a preponderance of units with preference for horizontal stimuli has also been found in the peripheral representation (50–90°) in visual I (area 17) by Kalia & Whitteridge (1973). It is quite possible that these ‘long-field’ units do have other specialized properties which were not detected and may not be apparent in the anaesthetized animal.

The map in visual III

Our map of V III fits reasonably well with the limits of area 19 as described by Otsuka & Hasler (1962) for their data, and with our material by using their criteria. Even though Allman & Kass (1975) claim that in the owl monkey area 19 contains more than one separate map of the visual field, it seems clear that there is not room for more than one map of the visual field in area 19 in the cat. As with area 18, however, the presence of ‘islands’ makes its map far from simple.

At present the significance of the ‘islands’ in V II and V III escapes us, and speculation is unprofitable.

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