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SECOND AND THIRD VISUAL AREAS OF THE CAT: INTERINDIVIDUAL VARIABILITY IN RETINOTOPIC ARRANGEMENT AND CORTICAL LOCATION

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SUMMARY

1. The cortical location and the retinotopic arrangement of the second (V2) and third (V3) visual areas in the cat have been investigated with single and multiple unit recordings in anaesthetized and immobilized animals.

2. V2 and V3 are arranged side by side anterior and medial to V1 and occupy the lateral gyrus and the postlateral sulcus. In addition, V2 spreads to postlateral parts of the lateral sulcus and, occasionally, to the posterior suprasylvian gyrus. The contralateral lower hemifield is represented on the lateral gyrus, the area centralis and the horizontal meridian are found in most animals in the anterior part of the postlateral sulcus, and the representation of the upper hemifield occupies the posterior part of the postlateral sulcus.

3. The detailed retinotopic arrangement of the visual field maps shows two characteristic features. First, the retinotopy at the V2/V3 border differs between lower and upper hemifield. In the lower hemifield the periphery of the fields is represented, whereas in the upper hemifield the border between the representations is formed by a sector running along the horizontal meridian about 5–10 degrees in the upper hemifield. Thus the lower field arrangement resembles that of rodents, and the upper field arrangement is similar to that of primates. Secondly, the periphery of a part of the visual field is not continuously represented, but forms patches or islands (Donaldson & Whitteridge, 1977). The islands are bounded by visual field representations closer to the vertical meridian. The way the visual field is represented at the border between V2 and V3 introduces discontinuities into the visual field maps: adjacent parts of the visual field are not represented adjacently in these two prestriate areas.

4. Cortical location and detailed retinotopic arrangement vary considerably from animal to animal, so that a representative map of V2 and V3 cannot be constructed. For example, the representation of the periphery of the horizontal meridian may be located either in the anterior portion of the postlateral sulcus or some mm more posteriorly, where the sulcus turns laterally. The representation of the area centralis in V3 is found either at the transition zone between lateral and postlateral sulcus, on the posterior suprasylvian gyrus, or in the posterior part of the postlateral sulcus.

5. The entire hemifield is represented in V2 at least in some animals. In V3 the uppermost part of the vertical meridian seems not to be represented. In other animals

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only a restricted part of the contralateral visual field is represented in V2 or in V3. In these cases the receptive fields cover not more than 50 degrees out in the lower hemifield or on the horizontal meridian. In a few cases the periphery of the horizontal meridian and the upper hemifield are not at all represented in V3, or only in an incomplete manner.

6. The magnification factors (Daniel & Whitteridge, 1961) become progressively smaller from V1 to V2 to V3. Hence cortical volume occupied decreases from V1 to V3. In V1 and in V2 the magnification is highest along the lower vertical meridian. In V2 the magnification along the horizontal meridian is the smallest, whereas in V1 the magnification decreases progressively from the lower vertical, to the horizontal and to the upper vertical meridian. The relationship between retinal ganglion cell densities and cortical magnification factors is discussed.

INTRODUCTION

In the last years it has been found that many more than three visual areas are located in the neocortex of cat (Palmer, Rosenquist & Tusa, 1978) and monkey (Allman & Kaas, 1974, 1975, 1976; Zeki, 1969, 1975; van Essen & Zeki, 1978). The functional properties of the cells in the various areas differ (Hubel & Wiesel, 1962, 1965; Zeki, 1975, 1978) and suggestions have been made on the contributions of these areas to the analysis of the visual surroundings of an animal (Sprague, Levy, Di-Berardino & Berlucchi, 1977; Zeki, 1978).

In spite of the increasing knowledge on the processing of afferent visual information in the neocortex, some of the basic principles essential for the participation of these areas in the analysis of the visual world are still unclear. For example, only little is known of the preciseness of the retinotopy and the spatial arrangement of functionally specific cells within the visual areas outside the primary visual area (V1) in the cat. Therefore, in order to arrive at a better understanding of how and what these areas contribute to visual perception, we have begun to study these parameters throughout the second (V2) and third visual area (V3). However, recordings from different parts of the representation of the retina in these areas posed problems because previous results on the retinotopy of V2 and V3 disagree considerably (Woolsey, Daube, Hoffmann, Kaas & Ladpli, 1967; Woolsey, 1971; Bilge, Bingle, Seneviratne & Whitteridge, 1967). The disagreement concerns the retinotopic arrangement at the lateral border of V2, the area of the visual field represented in V2 and the location of V3.

In preliminary experiments we found it difficult to place electrodes at a desired position in the visual field representation in a reproducible way. This was especially so for the peripheral parts of visual field representation and it made no difference what map we used as a guide. We therefore decided to study the retinotopy of V2 and V3 in the cat in detail in order to resolve the discrepancies mentioned above and to have a clearer base for our future single unit studies. Our results confirm earlier findings on a location of V3 immediately lateral to V2 (Hubel & Wiesel, 1965; Bilge *et al.* 1967; Donaldson & Whitteridge, 1977). In addition, we have worked out features of the retinotopy of V2 and V3 which were previously not known. Among them is

the finding that the representation of the visual field in V2 and V3 is split into two sectors. Another unexpected finding is that the cortical location and the retinotopic arrangement of V2 and V3 vary in a considerable manner from animal to animal. Some of the results have been published in a preliminary form (Beckmann & Albus, 1977; Albus & Beckmann, 1978).

METHODS

The experiments were performed in twenty-three adult cats. The animals received preoperatively an I.M. injection of prednisolone (5 mg Solu-Decortin-H), atropine (0·2 ml. of a 1% solution) and chlorpromazine (Megaphen 1 mg/kg). Anaesthesia was started either by pentobarbitone (Nembutal 35 mg/kg I.P.) or by ketamin-base (Ketanest 15 mg/kg) and was maintained by a continuous infusion of pentobarbitone (3·5 mg/kg.hr). In addition, the ketamin group was artificially respirated with a mixture of $N_2O/O_2/CO_2$ (72·5%/25%/2·5%). Muscular relaxation was started with an initial injection of 20 mg, and maintained by an infusion of gallamine triethiodide (Flaxedil 40 mg/hr). Drugs were applied in Ringer solution and the total fluid volume was 6 ml./hr. Rectal temperature and end-tidal concentration of CO_2 were permanently controlled and held constant between 37 and 38 °C, and between 3·6 and 4%, respectively. The animal was fixed into a stereotaxic instrument which was 12·5 degrees downward so as to make the visual axis of the cat's eye approximately horizontal (Bishop, Kozak & Vakkur, 1962). The cortex was covered with Agar (2·5% in Ringer solution). Glass-insulated tungsten wires having exposed tips of 10–15 μm were used as electrodes. These recorded the activity of several neurones simultaneously and sometimes isolated individual neurones as well. The distance between single penetrations was 1 mm and in some regions of the cortex 0·5 mm, especially at the transition zone from V2 to V3. This zone was grossly localized after the first experiments near the lateral edge of the lateral gyrus and in the postlateral sulcus. The representations of the lower hemifield and of the horizontal meridian were mapped with penetrations perpendicular to the horizontal plane of the Horsley–Clarke system. For mapping the representation of the upper hemifield, the electrode holder was inclined posteriorly by 25 degrees, so that the electrode penetrated the posterior occipital cortex from posterodorsal to anteroventral (Fig. 1*A*). Cortical activity was recorded every 500 μm, and every 100–200 μm at the transition zone from V2 to V3. Light stimuli of different shapes were projected onto a perimeter in order to determine the part of the visual field from which the respective clusters were activated. The perimeter was 0·5 m from the cat's eye and the cat's optics were corrected for that distance with contact lenses. The blind spot with issuing vessels was repeatedly projected during the experiment onto the perimeter through a reversible ophthalmoscope. The cortical regions of particular interest in this study are shown in Fig. 1*A*. The right hemisphere of a cat's brain is seen from above. We have explored the lateral gyrus, the lateral sulcus, the postlateral gyrus, the postlateral sulcus, and the posterior suprasylvian gyrus. The anterior portion and the posterolateral portion of the postlateral gyrus and sulcus have been labelled by *a* and by *p*, respectively. Outline drawings of histological sections, two made in a frontal plane (*b*, *c*) and one in a parasagittal plane (*a*) are reproduced in order to show the cortical landmarks which will appear on the visual field maps. We have indicated the medial and the lateral edge of the lateral and postlateral gyrus and the medial edge of the posterior suprasylvian gyrus. In the parasagittal sections, the posterior edge of the suprasylvian gyrus and the anterior and the posterior edge of the postlateral gyrus have been marked. In addition, the bottom of the lateral sulcus, of the postlateral sulcus and of the splenial sulcus are indicated.

After the experiments the receptive fields were transferred into a two dimensional co-ordinate system of the visual field. We have chosen a rectangular system (Mercator projection, Fig. 1*C*). The difference with a spherical polar co-ordinate system used by others (Tusa, Palmer & Rosenquist, 1978) is significant only in the very periphery of the visual field representation (see also Bishop *et al.* 1962). The co-ordinates of the system are termed isoelevation and isoazimuth. Positive elevations refer to the representation of the upper hemifield, negative elevations refer to the representation of the lower hemifield. Positive azimuths indicate positions in the contralateral hemifield, negative azimuths indicate positions in the ipsilateral hemifield.

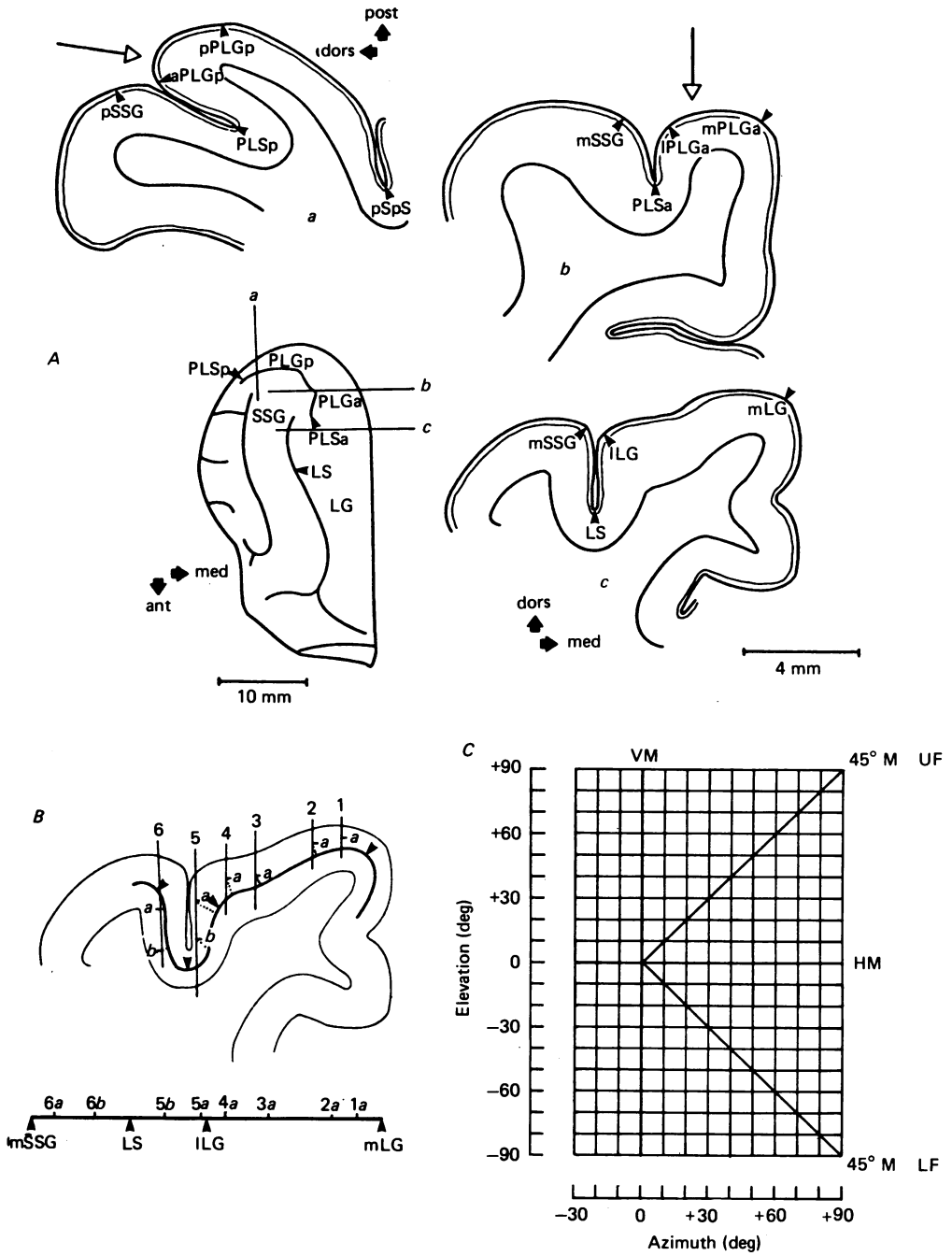

Fig. 1. *A*, cortical landmarks *in situ*. The right hemisphere of a cat's brain is seen from above. Outline drawings of histological sections made at three levels (*a*, *b*, *c*) are reproduced. One section is made in a parasagittal plane (*a*, top left), two sections are made in a frontal plane (*b*, *c*, top right and bottom right). In this and all the following Figures the parasagittal sections are oriented in such a way that the dorsal part of the

The position of the zero (vertical) meridian was calculated from the mean position of binocular receptive fields in or near the area centralis (Nikara, Bishop & Pettigrew, 1968). Its course was estimated on the basis of receptive fields located on the border between V1 and V2 a larger part of which was plotted in every animal. The functional centre of the area centralis was determined by joining the zero meridian with the position line through the centre of the blind spot. A constant angle for the position of the blind spot centre was used for all animals (B = 22·2 degrees; see Bishop *et al.* 1962). This angle was drawn with reference to a line running perpendicular to the vertical meridian and through the centre of the blind spot. The true horizontal of the cat's eye (fixation plane) is then given by a line perpendicular to the vertical meridian and running through the functional centre of the area centralis. As an additional control for eye rotation, binocular receptive fields were used which were located in the periphery of the visual field.

The animals were sacrificed after the experiment by an overdose of pentobarbitone and perfused through the heart by formalin (4%). Histological sections 60 μm thick were made either in frontal or in parasagittal planes and stained alternatively with Cresyl Violet, or Luxol Fast Blue. The plane of the frontal sections is perpendicular to the course of the lateral sulcus, and of the anterior portion of the postlateral sulcus. The plane of the parasagittal sections with respect to the course of the posterior portion of the postlateral sulcus is first nearly perpendicular and becomes oblique with increasing distance from the midline.

Electrode tracks were reconstructed using electrolytic lesions made during the experiments as landmarks. Recording positions along tracks (Fig. 1*B*, top) were projected along the radial cell columns onto a reference line which was drawn halfway between bottom of the sixth layer and top of the first layer: the reference line was then stretched and in addition to recording points cortical landmarks were noted on it (Fig. 1*B*, bottom). Thus each reference line represents the whole of recordings made in one frontal (or parasagittal) plane. A position map was then prepared on the basis of all reference lines obtained in one animal. The reference lines were aligned with respect to the medial edge of the lateral gyrus, or with respect to the bottom of the postlateral sulcus. The result of the stretching procedure is demonstrated in Fig. 2. Here for one animal all the cortical landmarks are shown as they would appear if the cortex were stretched out. The direction of the stretching is indicated on the surface view of a right hemisphere by the arrows. For frontal sections it is away from the medial edge of the lateral gyrus to lateral, or away from the bottom of the postlateral sulcus to medial or to lateral. For parasagittal sections it is away from the bottom of the postlateral sulcus to posterior or to anterior. When a position map was prepared from parasagittal sections, the distances between the reference lines were corrected (enlarged) for the obliquity of the postlateral gyrus (posterior portion). This was estimated with respect to the horizontal plane of the Horsley–Clarke reference system. The position maps were finally transformed into visual field maps by noting for each recording point the visual field co-ordinates of its receptive field and by connecting points having the same elevation or the same azimuth by lines (isoelevation or isoazimuth lines). Each map was constructed on the basis of at least 120 receptive field plots. These were sampled in recording sessions lasting 24–36 hr. Due to the interindividual variations we were forced to map with a relatively high recording density. Therefore, in one animal not the entire visual field, but only the representation of either the lower hemifield or of the horizontal meridian and the upper hemifield was completely mapped. In the following results, therefore the retinotopic arrangement will be discussed separately for the representation of the lower hemifield, of the area centralis and the horizontal meridian, and finally of the upper hemifield.

Abbreviations used in the Figures: LG, lateral gyrus; LS, lateral sulcus; PLG, postlateral

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cortex is to the left and the posterior part of the cortex (i.e. the tentorial surface of the postlateral gyrus) upwards. The abbreviations of the cortical gyri and sulci are explained in the text. The arrows in *b* and *a* give the direction of the electrode track perpendicular, and oblique respectively, with respect to the horizontal plane of the Horsley–Clarke co-ordinate system. *B*, reference line (thicker line) with recording positions *in situ* (top) and stretched (bottom). Further explanations see text. *C*, rectangular co-ordinate system of the visual field (Mercator projection). The upper and lower oblique meridians are indicated in addition to the isoelevation and isoazimuth lines.

gyrus; PLS, postlateral sulcus; mLG and lLG, medial and lateral edge of the lateral gyrus; mPLGa and lPLGa, medial and lateral edge of the postlateral gyrus (anterior portion); aPLGp and pPLGp, anterior and posterior edge of the postlateral gyrus (posterior portion); mSSG and pSSG, medial and posterior edge of the suprasylvian gyrus; pSpS, splenial sulcus (posterior part).

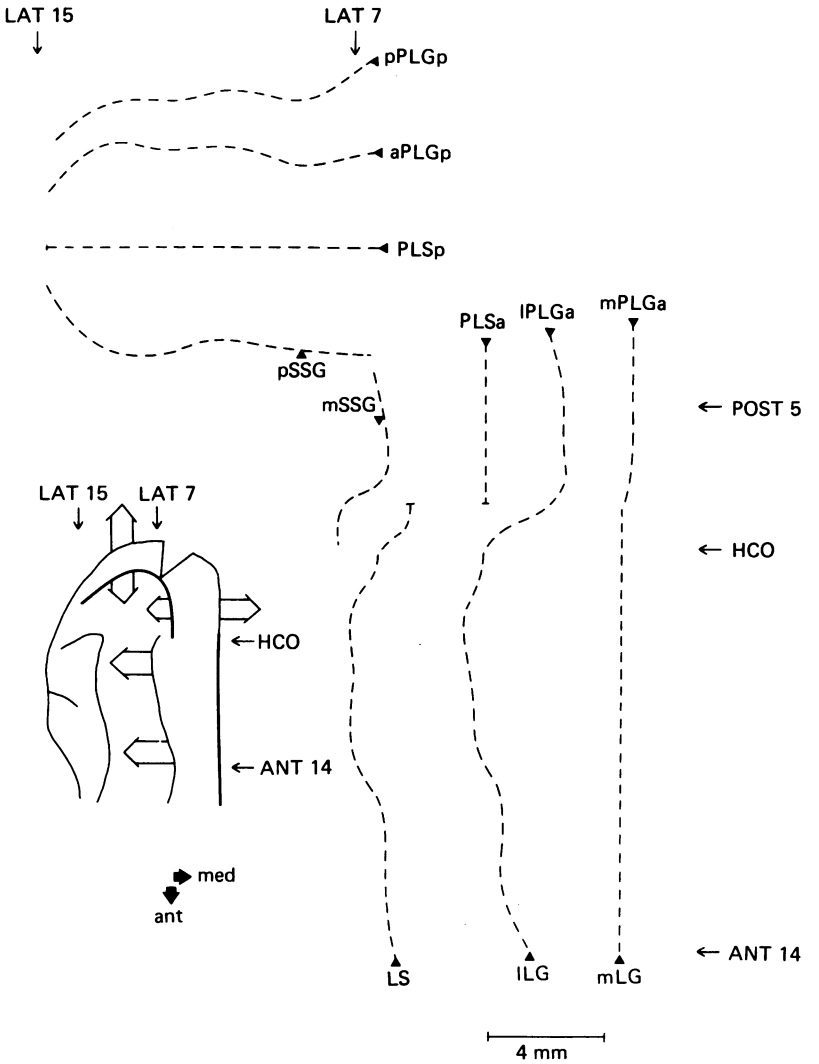


Fig. 2. The cortical landmarks as appearing on an extended surface of a right hemisphere. The direction into which the cortical surface is stretched is given by arrows on a surface view of a right hemisphere (inset). The frontal sections are stretched away from the medial edge of the lateral gyrus laterally, and away from the anterior portion of the postlateral sulcus laterally and medially. The parasagittal sections are stretched anteriorly and posteriorly, away from the posterior portion of the postlateral sulcus. Medial edge of the lateral gyrus and bottom of the postlateral sulcus therefore are used as fixed points (heavier in drawing). HCO, interaural plane of the Horsley–Clarke co-ordinate system. ANT, indicates distance of frontal planes anterior from interaural plane (mm). POST, indicates distance of frontal planes posterior from interaural plane (mm). LAT, indicates distance of parasagittal planes from the mid line of the brain (mm).

RESULTS

Our experimental material consists of five maps of the lower hemifield, twelve complete maps of the area centralis and of the horizontal meridian and seven complete maps of the upper hemifield. In addition in five animals only parts of the lower hemifield were mapped. For comparison parts of the representation of the visual field in V1 were also mapped in four animals. Characteristic features of the retinotopic arrangement and the cortical location of V2 and V3 become immediately obvious when the individual maps are compared. Among these are the approximate course of

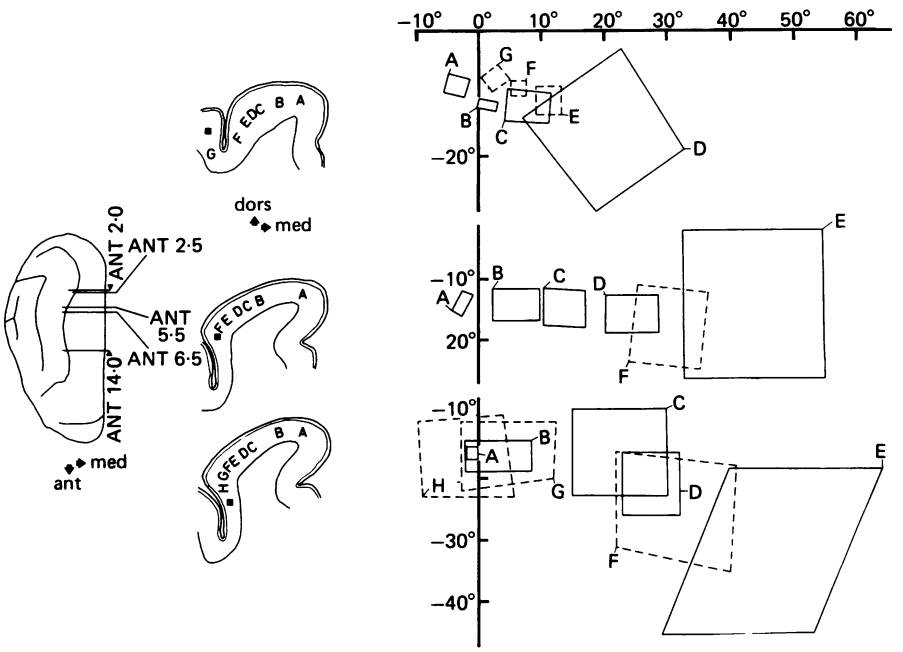


Fig. 3. Mapping of the representation of the lower hemifield in V2 and V3. The lateral sulcus and the lateral gyrus were explored between ANT 2 and ANT 14·5. Recording positions in the cortex are indicated by letters on outline drawings of frontal histological sections at ANT 2·5, 5·5 and 6·5. The related contralateral receptive fields are reproduced on the right-hand side in schematic drawings of the left lower hemifield. This Figure, and all the following Figures of this type are arranged in such a way that the reader faces the experimental situation: the right hemisphere of the animal is to the left, and the left visual hemifield of the animal to the right. Receptive fields with continuous lines are from V2, that with interrupted lines from V3. Only about 50% of all receptive fields recorded in each frontal plane are reproduced in this and all the following figures of the same type.

the isoelevation and isoazimuth lines across the cortex, the rough cortical location of the different parts of the representations and the volume of cortex representing unit area in the visual field. Nevertheless, considerable differences between the maps were also noted. These concerned the detailed retinotopic arrangement at the representation of the visual field periphery, and the cortical location of some parts of the representation. Due to these variations, a map of V2 and V3 representative for the cat could not be constructed.

In each of the following paragraphs characteristic features of the retinotopic arrangement are worked out first, based on animals in which V2 and V3 are organized in the simplest and clearest way. Then the major modifications of this basic retinotopic scheme will be presented. The basic scheme and its modifications will give an idea of how the visual field is represented in V2 and in V3 of the cat.

(1) The representation of the lower hemifield

The representation of the lower hemifield in V2 and V3 is located on top of the lateral gyrus and on the medial bank of the lateral sulcus. Some representative examples out of many penetrations made through this cortical region are reproduced in Fig. 3. At the medial edge of the lateral gyrus the receptive fields are located on the vertical meridian and/or in the ipsilateral hemifield (Fig. 3, fields A). This area represents the border between V1 and V2. Moving across the lateral gyrus, the receptive field positions shift into the periphery of the contralateral lower hemifield and slightly downwards reaching eccentricities of 50 degrees (Fig. 3, fields E). Further laterally on the gyrus, the fields reverse their progression and shift back to the vertical meridian. At ANT 5·5 the reversal is incomplete since the corresponding part of V3 is displaced to anterior and therefore, not detected by a mediolateral movement of the electrode (see Fig. 4).

These few examples indicate a third representation of the contralateral hemifield immediately lateral from V2. In the map (Fig. 4) the vertical meridian at the V1/V2 border is running along the medial edge of the lateral gyrus, and the vertical meridian in V3 is located along the lateral edge of the gyrus. The latter also marks the lateral border of the visually excitable cortex. In between the two representations of the vertical meridian (in V1/V2, and V3) azimuths out to 15 degrees are represented anteriorly and azimuths out to 50 degrees posteriorly on the gyrus. Here the azimuth lines 20–40 form complete contours around azimuth 50. Since in V3 the centre positions of the receptive fields did not always reach the vertical meridian, the isoazimuth zero in V3 is not drawn as a continuous line. The field areas, however, mostly overlapped the vertical meridian into the ipsilateral hemifield.

The spatial arrangement of isoazimuth and isoelevation lines confirms that the representation of the contralateral hemifield is located immediately lateral from V2. V3 is considerably smaller than V2. The border between V2 and V3 is formed by the periphery of the lower hemifield. Here a peculiar topographical arrangement is found. Crossing the representation 5–10 degrees below the horizontal meridian, only eccentricities of less than 15 degrees are recorded. 10–30 degrees below the horizontal meridian, the receptive fields cover eccentricities of more than 50 degrees. Since further anterior the distance between the vertical meridian and the peripheral field locations again decreases (to about 15 degrees) the lower hemifield representation forms an 'island' bounded by areas of the visual field closer to the vertical meridian. Such islands in V2 and V3 have been recently reported also by Donaldson & Whitteridge (1977). This type of organization implies that the representation of the lower field periphery is not continuous with the representation of the horizontal meridian located posteriorly (not shown here). Both are connected across parts of the visual field closer to the vertical meridian, i.e. paracentral parts of the visual field. The map of two other cases (not shown here) were similar to that of Fig. 4. There were

minor differences in that the most peripherally located fields were 40 degrees distant from the vertical meridian (50 degrees in Fig. 4) and V3 became wider at its anterior end (and not smaller as in Fig. 4). In one of three further cases in which only the outer periphery of the lower vertical meridian was mapped, V2 and V3 occupied parts on the medial bank of the lateral gyrus, thus both forming the anterior border of V1.

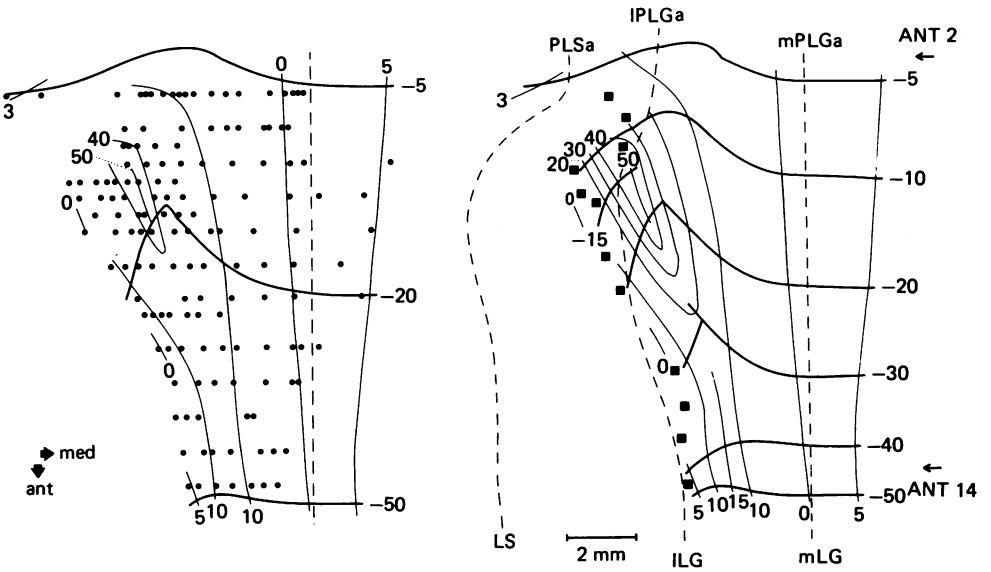
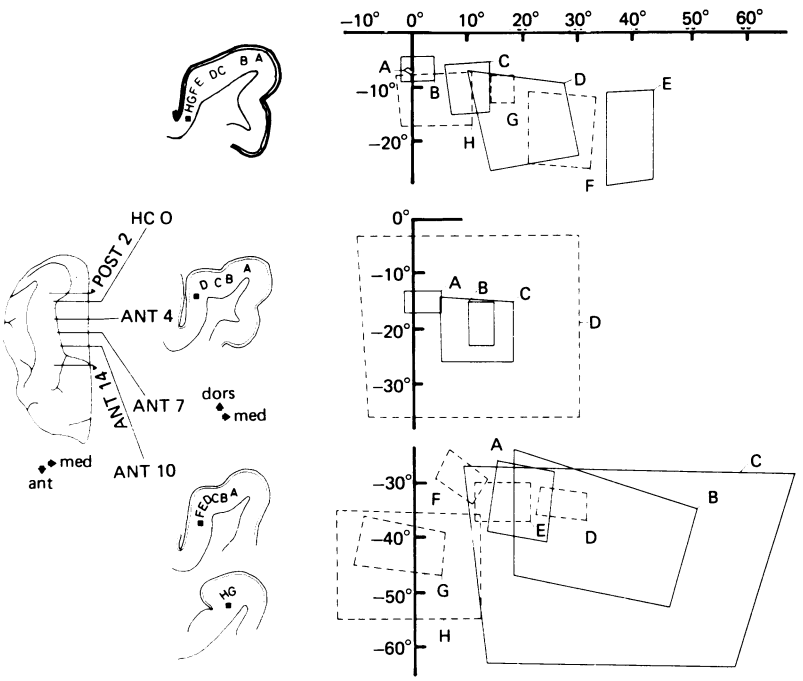


Fig. 4. Map of the representation of the lower hemifield in V2 and V3. The visual field map is shown on the right-hand side. The thicker continuous lines are isoelevations and the numbers beside them indicate the distance from the horizontal meridian (in degrees of arc). The thinner continuous lines are isoazimuths and the numbers beside them indicate the distance from the vertical meridian (in degrees of arc) in the contralateral hemifield. The thin interrupted lines indicate the cortical landmarks within the map (see Figs. 1*A* and Fig. 2). As can be seen, the isoelevation lines run across the medial edge of the lateral gyrus, turn to posterior on top of the gyrus and then back to anterior. The isoazimuth lines predominantly run from posterior to anterior. The dark squares indicate cortical positions from which nonvisual activity was recorded. The map is constructed on the basis of 145 receptive fields the recording positions of which are schematically reproduced by points in the position map (left-hand side). In this and all other position maps about 20% of the recordings are not considered. These were either recordings from nonvisual cortex or receptive field plots from cortical sites which had already been explored by another penetration (e.g. parallel penetrations in the same frontal plane through the medial bank of the lateral sulcus). All visual field maps are constructed from contralateral receptive fields; only some ipsilateral fields were used. Further explanations see Fig. 2.

The two remaining maps were differently organized. Instead of one, they had two islands which represented adjacent parts of the lower hemifield. Recordings from the lateral gyrus of one of these cases are shown in Fig. 5. 10–15 degrees below the horizontal meridian, the receptive fields reach eccentricities of 40 degrees. 25 degrees below the horizontal meridian, the outward progression of the fields stops 15 degrees distant from the vertical meridian. Further lateral on the gyrus there is no clear reversal and large fields are recorded which overlap the vertical meridian into the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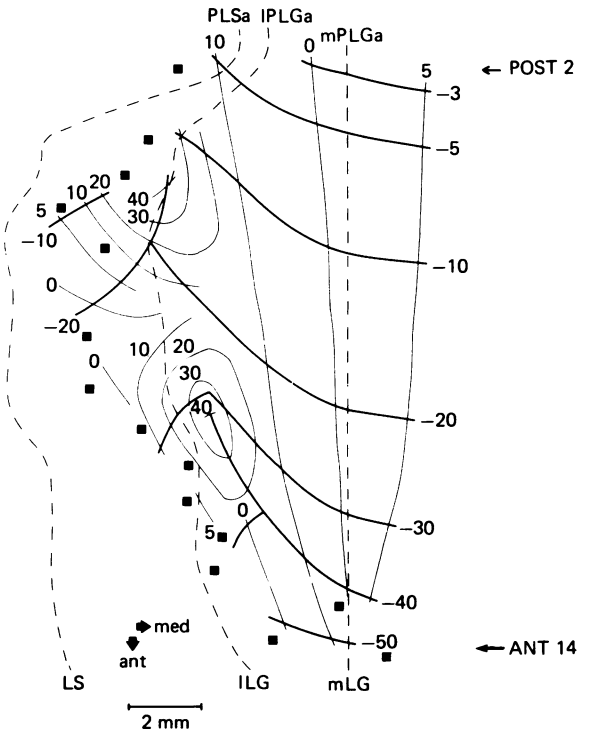
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ipsilateral hemifield up to 10 degrees (field D at ANT 4). 30 to 40 degrees below the horizontal meridian, the receptive field centres again reach azimuths of more than 40 degrees. These penetrations suggest that a sector of the visual field close to the vertical meridian has protruded in between the representation of the periphery. In fact, the visual field map of this case shows that the periphery of the lower hemifield is represented at two cortical sites which are about 6 mm distant from each other. At these sites the periphery is organized in the form of islands which are bounded by parts of the visual field closer to the vertical meridian. One island contains the periphery 10 to 25 degrees below the horizontal meridian, the other island contains the periphery 25–40 degrees below the horizontal meridian. Between the islands a part of the vertical meridian in V3 is represented. The border between V2 and V3 runs nearly straight on the lateral gyrus along its lateral edge. The visual field positions at the border, however, take a rather curved path through the lower hemifield: from posterior to anterior they occupy first the periphery of the lower hemifield, then approach the vertical meridian, shift back into the periphery and finally back again towards the vertical meridian.

Receptive fields even larger than field D (ANT 4, Fig. 5) were detected in this and other animals. Some of these fields overlap the vertical meridian into the ipsilateral hemifield by more than 30 degrees. Such fields were found only in parts of the representation just anterior and posterior from the periphery islands.

(2) The representations of the area centralis and of the horizontal meridian

The representations of the area centralis and of the horizontal meridian in V2 and V3 occupy the anterior portions of the postlateral gyrus and sulcus, and occasionally a small strip on the posterior suprasylvian gyrus. The complete map of one case is shown in Fig. 6. The vertical meridian at the V1/V2 border (isoazimuth line zero) runs along the postlateral gyrus. The horizontal meridian in V2 and V3 representing the fixation plane of the cat's eye (isoelevation line zero), runs across the postlateral gyrus and sulcus and ends on top of the posterior suprasylvian gyrus. The periphery of the meridian is located on the lateral bank of the postlateral sulcus. Here the azimuth lines 20 and 30 form complete contours around azimuth 40. Posterior from the representation of the horizontal meridian, paracentral parts of the upper hemifield are found. According to the spatial arrangement of isoazimuth, and isoelevation lines, a third representation of the area centralis and of the horizontal meridian is located immediately lateral from V2. The border between both areas is formed by the periphery of the horizontal meridian. As can be seen, the cortical volume occupied by the representations of the periphery of the horizontal

Fig. 5. Representation of the lower hemifield in V2 and V3. Top: the lateral gyrus and the lateral sulcus were explored between POST 2 and ANT 14. Recording positions in the cortex are indicated by letters on outline drawings of frontal histological sections at HC 0, ANT 4, 7 and 10. The related contralateral receptive fields are reproduced on the right-hand side in schematic drawings of the left visual hemifield. The receptive fields located on the vertical meridian at the V1/V2 border are not reproduced for ANT 7 and ANT 10. Further explanations see legend to Fig. 3. Bottom: map of the representation of the lower hemifield in V2 and V3. The various lines and the abbreviations have already been explained in the legend to Figs. 2 and 4. The map is constructed on the basis of 175 receptive fields.

meridian and of the area centralis in V3 is relatively small: it measures only 3 mm in a mediolateral and 1–2 mm in an anteroposterior direction, as compared to 9 and 4 mm, respectively, in V2. The periphery of the horizontal meridian is organized according to the same principle as the periphery of the lower hemifield: it forms an

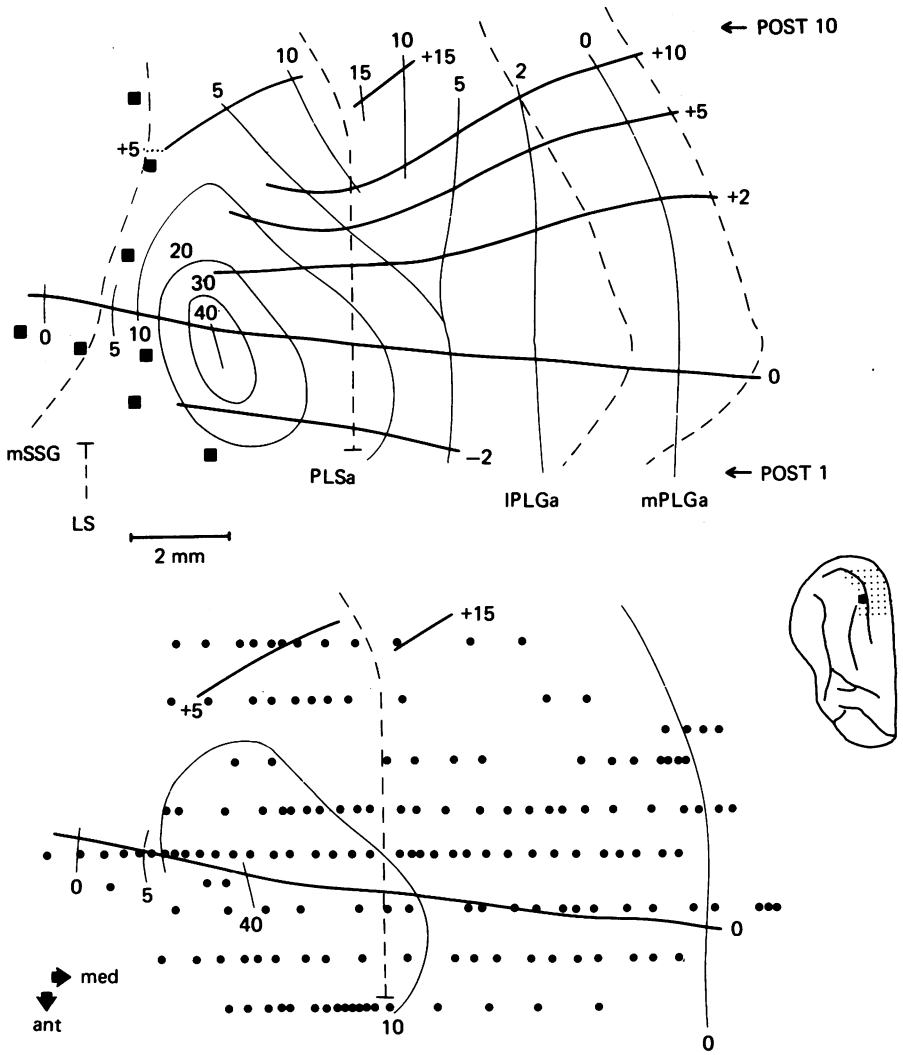


Fig. 6. Map of the representation of the area centralis and of the horizontal meridian in V2 and V3 (top). The map is constructed on the basis of 163 receptive fields, the cortical positions of which are indicated by points in the position map (bottom). Further explanations see legend to Figs. 2 and 4. The cortical area explored (small dots) and the location of the periphery of the horizontal meridian (dark point) are indicated on a surface view of a right hemisphere.

'island' bounded by paracentral parts of the lower and upper hemifield, i.e. by parts of the visual field closer to the vertical meridian. This means that the representation of the periphery of the horizontal meridian is not continouous with the periphery of

either upper or lower field. Another type of 'island' like representation is realized for the area centralis in V3. This has no continuity with adjacent parts of the lower and upper vertical meridian.

Two modifications of the basic retinotopic scheme are observed at this site of the representation: (1) the cortical location of parts of the representation varies; (2) the

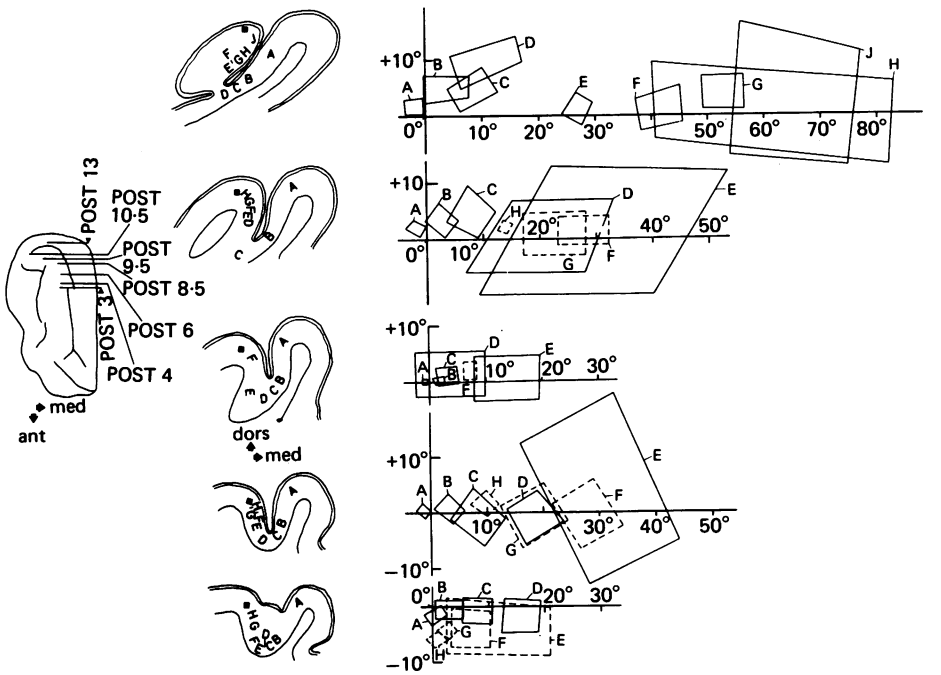


Fig. 7. Mapping the representation of the area centralis and of the horizontal meridian in V2 and V3. The brain was explored between POST 3 and POST 13. Outline drawings of frontal histological sections are reproduced for POST 4, 6, 8·5, 9·5, 10·5. The related receptive fields are shown on the right-hand side. Further explanations see legend to Fig. 3.

representation of the visual field in V3 is incomplete. Both modifications can occur in one animal. In five cats the representation of the periphery of the horizontal meridian is displaced to posterior. It is located at a site where the postlateral sulcus turns into a posterolateral direction. Two cases are demonstrated in Figs. 7 and 8. In one of these, the near periphery of the horizontal meridian (eccentricities less than 30 degrees) is located in the anterior part of the postlateral sulcus, on its lateral bank (Fig. 7; POST 6, fields E and F). Posterior to this small representation, paracentral parts of the horizontal meridian and of the upper hemifield are found (Fig. 7; POST 8·5). This indicates a somewhat restricted representation of the horizontal meridian, located at its 'normal' place (see Fig. 6). Still more posterior on the postlateral gyrus and in the sulcus, field positions have shifted into the upper hemifield (Fig. 7; POST 9·5 and POST 10·5, fields A–C, and A–D, respectively). On the lateral bank of the sulcus, however, the fields are not in the upper hemifield but still on the horizontal meridian, covering now eccentricities of more than 65 degrees (Fig. 7; POST 10·5,

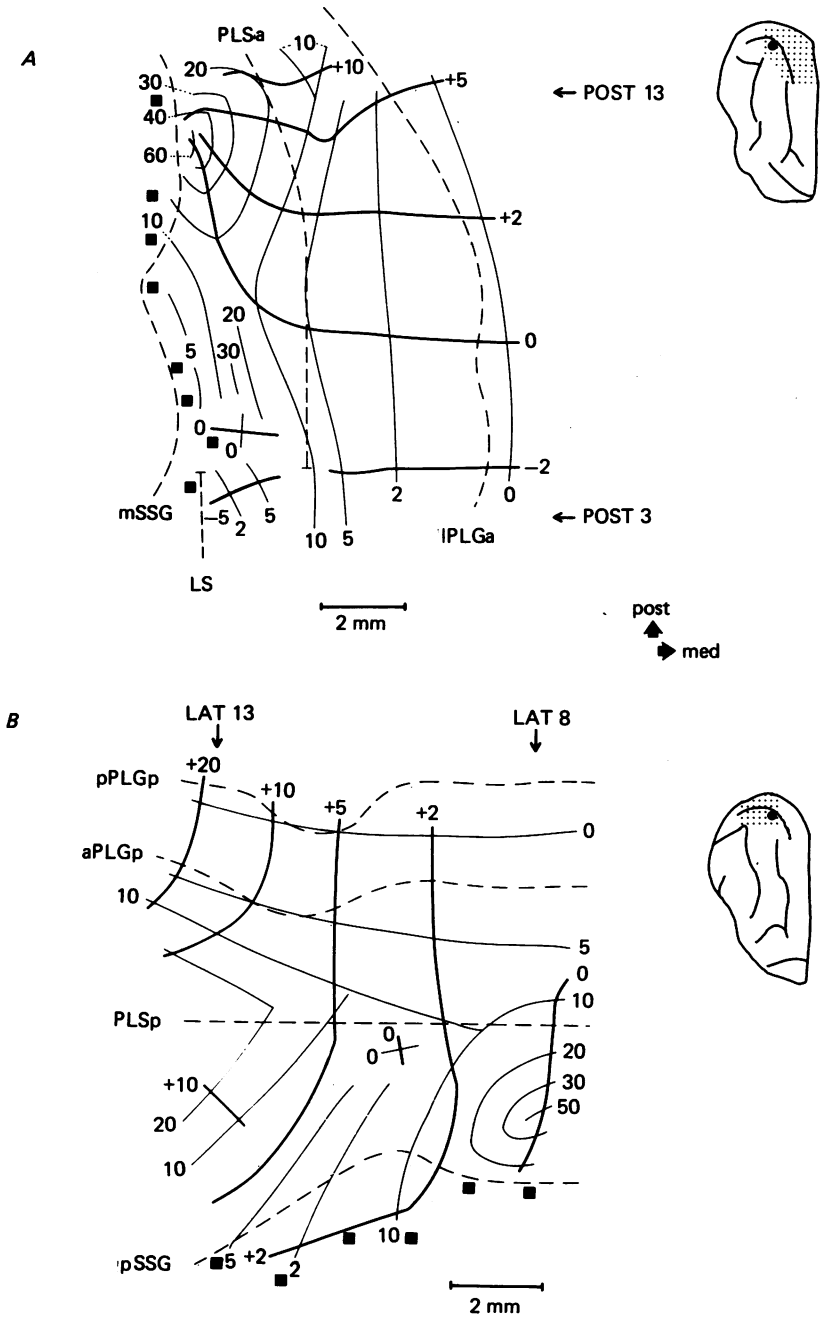


Fig. 8. Maps of the representation of the area centralis and of the horizontal meridian in V2 and V3. The visual field map in A is prepared on the basis of 156 receptive fields. The visual field map in B is constructed on the basis of 153 receptive fields. Further explanations see legend to Figs. 2 and 4. The area of the brain explored (small dots) and the approximate location of the periphery of the horizontal meridian (dark point) are indicated on a surface view of a right hemisphere for *A* (top) and *B* (bottom).

fields H and J). The map of this animal (Fig. 8*A*) shows that the isoelevation line zero follows this posterior displacement: it traverses first the V1/V2 border, turns then sharply to posterior and ends near the posterior edge of the suprasylvian gyrus. The map actually has two representations of the horizontal meridian, which both are organized in the form of an island. The larger of the two is located 11–12 mm posterior to the interaural plane and contains the entire meridian. The smaller representation

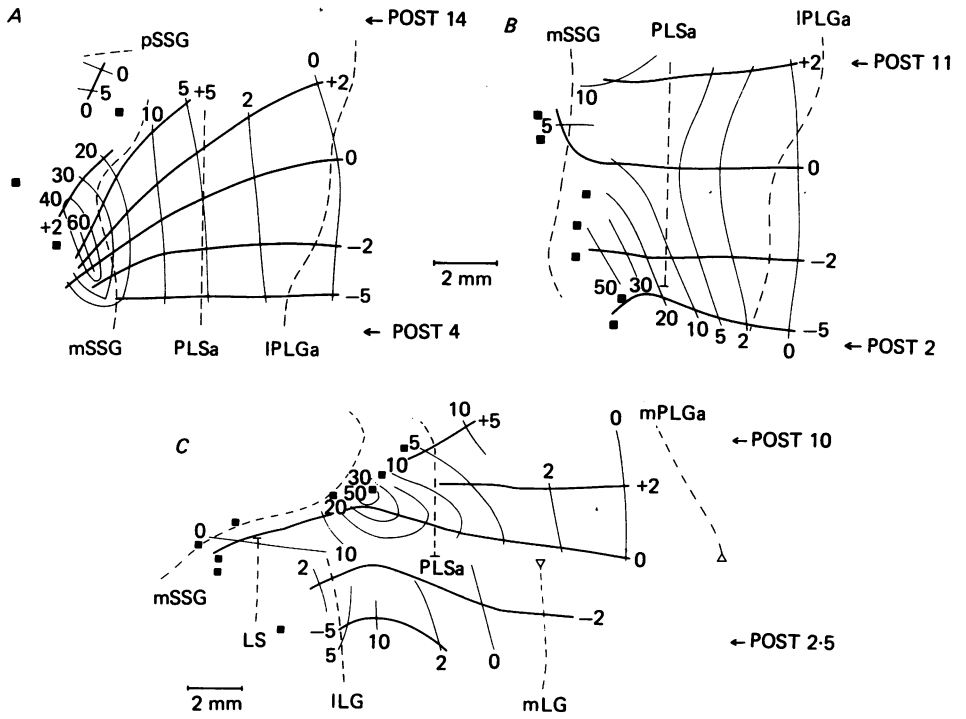


Fig. 9. Visual field maps of the representation of the area centralis and the horizontal meridian in V2 and V3. In *A* the brain was explored between POST 4 and POST 14 (104 receptive fields); in *B* between POST 2 and POST 11 (134 receptive fields); in *C* between POST 2·5 and POST 10 (120 receptive fields). Further explanations see text and legend to Figs. 2 and 4.

is found about 5 mm more anterior and covers only 30 degrees eccentricity. A reversal in receptive field progression indicating V3 occurs only at the periphery of the smaller of the two representations. Here the fields shift back towards the vertical meridian (Fig. 7; POST 4 and POST 6, fields E–H, F–H, respectively). The representation of the area centralis in V3 is displaced anteriorly so that it is located between the smaller representation of the horizontal meridian and the representation of paracentral parts of the lower hemifield in V3. In another case the periphery of the horizontal meridian is located on the anterior bank of the postlateral sulcus, i.e. in the posterior portion of the sulcus (Fig. 8*B*). Again the representation is organized in the form of an island. Lateral from the island the representations of paracentral parts of the upper hemifield in V2 and V3 emerge. V2 is located posterior and V3 anterior from the bottom of the postlateral sulcus (see next paragraph).

Further examples of modifications of the basic retinotopic scheme are demonstrated in Fig. 9. In one case (Fig. 9*A*) the representation of the area centralis in V3 on the

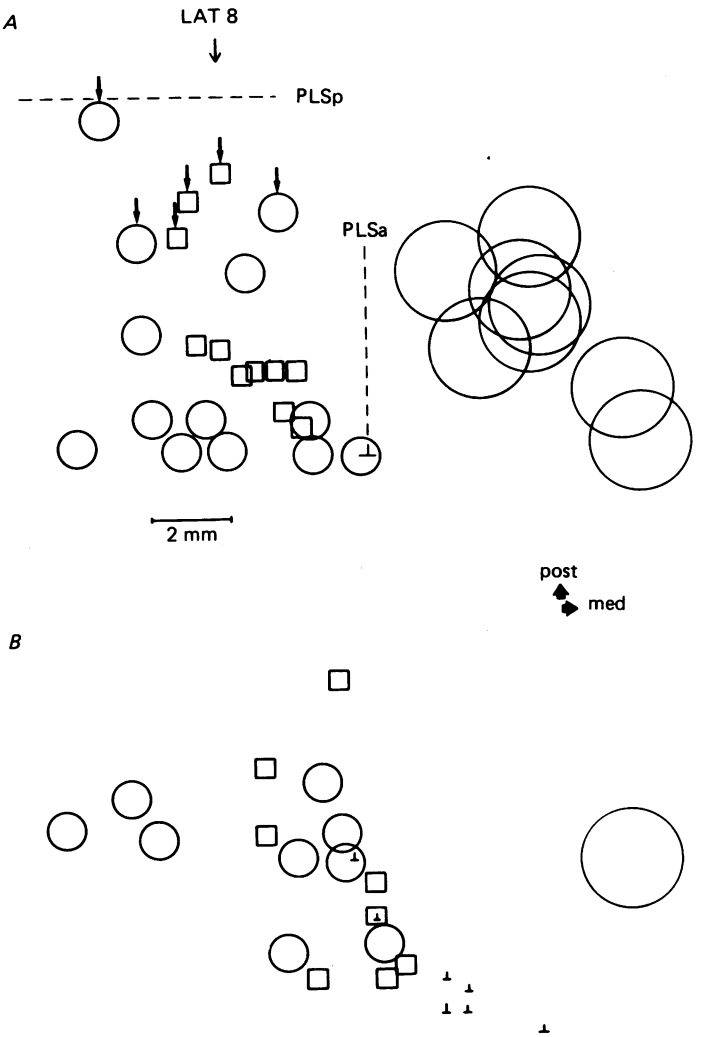


Fig. 10. The cortical locations of the representations of the area centralis and the periphery of the horizontal meridian in V2 and V3. The area centralis at the V1/V2 border is indicated by large diameter circles, that in V3 by small diameter circles. The horizontal meridian periphery at the V2/V3 border is given by open squares. *A*, representations arranged with respect to the anterior beginning of the postlateral sulcus. Representations marked by an arrow are located on the anterior bank of the postlateral sulcus (posterior portion). *B*, two of the representations (area centralis in V3 and horizontal meridian at the V2/V3 border) are arranged with respect to the cortical location of the third (area centralis at the V1/V2 border). For seven animals the location of the anterior beginning of the postlateral sulcus is given by ⊥.

posterior suprasylvian gyrus is displaced to posterior with respect to the periphery of the horizontal meridian. In another animal, the area centralis in V3 is located in the very posterior end of the lateral sulcus (Fig. 9*C*), i.e. it is displaced anteriorly

with respect to the horizontal meridian. The case is unique in that representations of the area centralis form a nearly continuous band across the transition zone between lateral and postlateral gyrus: clusters of cells having fields located in the centre of gaze are just anterior and medial as well as lateral from the posterior end of the lateral sulcus. Another patch containing centrally located fields is found just anterior from the postlateral sulcus. In a third animal, the periphery of the horizontal meridian in the postlateral sulcus is represented for V2 but not for V3 (Fig. 9*B*). At a cortical site normally occupied by this representation, only visually unresponsive clusters were recorded. Only a small paracentral area seems to be represented in V3, more posteriorly in the sulcus.

Our findings also suggest that in some animals the horizontal meridian is not completely represented in V2. In four animals (out of twelve in which the meridian was mapped) the receptive field centres reach out to eccentricities of only 40 degrees. Since the recording density in these cases is high (see Fig. 6), it is hardly possible that peripheral parts of the representation were missed.

In order to get an idea of the overall variability in the cortical location of the area centralis and of the horizontal meridian, we determined the locations with respect to a cortical landmark, the anterior beginning of the postlateral sulcus. This point can be reliably determined on histological sections. The result is shown in Fig. 10*A*. The representations of the area centralis at the border between V1 and V2 are found over a cortical area measuring 8 by 8 mm. All the representations are located medially from the bottom of the postlateral sulcus. The representations of the area centralis in V3 are distributed over a cortical area measuring 10 mm in an anteroposterior and 7 mm in a mediolateral direction. The representations are located laterally from the anterior portion, and anteriorly from the posterior portion of the postlateral sulcus. The representations of the periphery of the horizontal meridian are located also laterally and anteriorly from the postlateral sulcus, the maximal anteroposterior distance between two representations being 7 mm. The latter representations seem to form two clusters, one of which is located at the anterior bank, and the other on the lateral bank of the postlateral sulcus.

Considerable variability is also found when the various representations are arranged with respect to the interaural plane of the Horsley–Clarke co-ordinate system. Here the maximal distances between two single representations measured in an anteroposterior direction is 8 mm for the area centralis at the V1/V2 border, 9 mm for the periphery of the horizontal meridian and 7 mm for the area centralis in V3. In order to exclude a possible contribution to the variability by interindividual variations in the interaural plane (Tusa *et al.* 1978), the representations were arranged with respect to the cortical location of the representation of the area centralis at the V1/V2 border (Fig. 10*B*). As can be seen, there is no reasonable order in this arrangement. On the basis of our findings, a weak relationship between the cortical location of some parts of the representation and the course of the postlateral sulcus might be suggested. However, the cortical location of the visual field points considered is difficult to predict by using an external co-ordinate system, or by using the spatial relationship of these points in the map.

(3) The representation of the upper hemifield

The representations of the contralateral upper hemifield in V2 and V3 occupy the posterior portion of the postlateral sulcus and gyrus and occasionally a small strip on the posterior suprasylvian gyrus. Generally the receptive field positions shift from the vertical meridian into the periphery of the upper hemifield and then back to the vertical meridian when the cortex is crossed from posterior to anterior. Some repre-

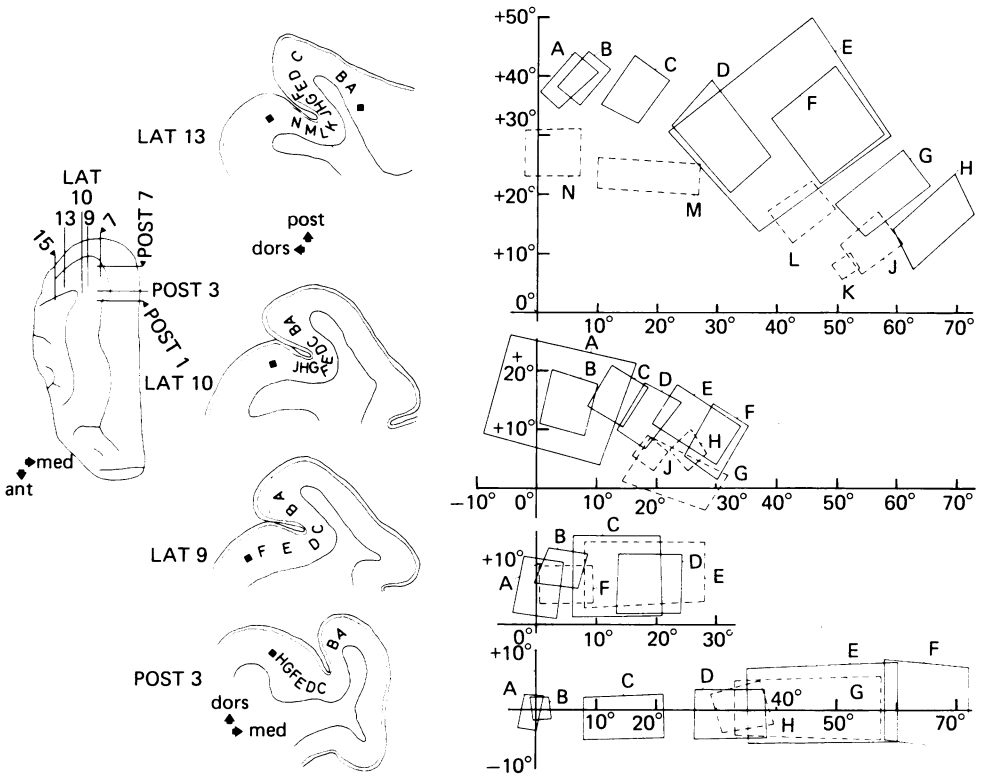


Fig. 11. Mapping the representation of the area centralis, of the horizontal meridian and of the upper hemifield in V2 and V3. The anterior portion of the postlateral sulcus was explored between POST 1 and POST 7 and the recordings in one frontal plane (POST 3) are reproduced. The posterior portion of the postlateral sulcus was explored between 7 and 15 mm lateral from the midline, and the recordings in three parasagittal planes (LAT 9, 10 and 13) are reproduced. Further explanations see legend to Fig. 3 and Fig. 1*A*.

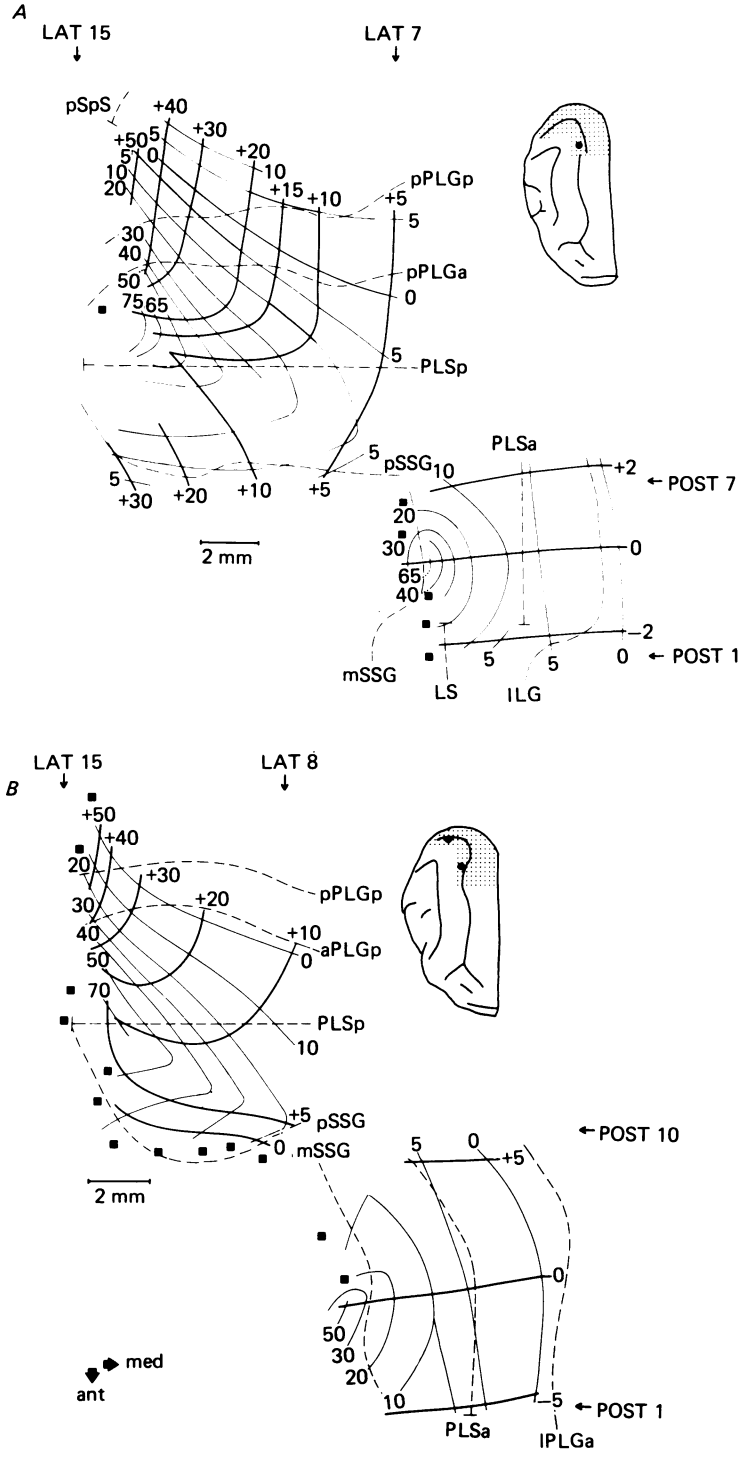
sentative penetrations through this posterior part of the brain are reproduced in Fig. 11. Medially in the cortical area explored, the receptive fields reach eccentricities of only 20 degrees (LAT 9). More lateral in the cortex, the receptive fields cover progressively more peripheral parts of the upper hemifield, and besides the outward movement also a trend towards the horizontal meridian is observed. 10 mm lateral the mid line (at position 6) a receptive field is plotted which even overlaps the horizontal meridian into the lower hemifield. The trend towards the horizontal meridian is observed also at other lateral levels not reproduced.

These penetrations suggest two separate representations of the upper hemifield, anteriorly from V1; they suggest further that the retinotopic arrangement at the V2/V3 border is different between lower and upper field representation. The map (Fig. 12*A*) confirms this. According to the spatial arrangement of isoazimuth and isoelevation lines (for a detailed description see legend to Fig. 12*A*) V2 is located on the posterior bank, and V3 on the anterior bank of the postlateral sulcus. The border between the two representations runs along the bottom of the sulcus and is formed by a sector in the upper hemifield about 5–10 degrees above the horizontal meridian. The adjacent part of the visual field, i.e. the horizontal meridian is located some mm distant in the cortex: in the anterior portion of the postlateral sulcus (Fig. 12*A*; lower right part of the map). Here the receptive fields cover eccentricities out to 70 degrees (Fig. 11; POST 3, field F). As can be seen, this arrangement causes a further discontinuity in the representation of the visual field in V2 and V3 (see also retinotopy of the lower hemifield): adjacent parts of the visual field are represented not adjacently in a cortical visual area. Both parts of the representation of the periphery are connected across the representation of paracentral parts of the upper hemifield and of the horizontal meridian.

As a major variation, the third representation of the upper hemifield is incompletely or not at all developed in some animals. One example of the latter type is reproduced in Fig. 12*B*. The upper field representation in V2 extends across the postlateral sulcus anteriorly and occupies most of its anterior bank. The anterior border of V2 is formed by the horizontal meridian, which also marks the border between visual and non-visual cortex. Accordingly, a cortical region which in other animals is occupied by the representation of the upper hemifield in V3 here contains the horizontal meridian and adjacent parts of the upper hemifield in V2. The anterior portion of the postlateral sulcus was explored as well in this case (Fig. 12*B*, lower right part of the map). At this cortical site the receptive fields also cover a large part of the horizontal meridian, the periphery of the meridian being located near the medial edge of the posterior suprasylvian gyrus. Therefore the representation of the meridian is split into two parts: one part is located in the anterior portion, the other part is located in the posterior portion of the postlateral sulcus, mainly on its anterior bank.

A case with an incomplete third representation is shown in Fig. 13*A*. The area of the visual field covered is only 30 degrees on the horizontal meridian and 15 degrees on the upper vertical meridian. The map is, however, not orderly since parts of the upper vertical meridian are bounded medially by paracentral parts and laterally by more peripheral parts of the upper hemifield.

A small fourth representation of the upper hemifield is found in this animal in the very lateral bottom of the postlateral sulcus. Here the receptive fields reverse their progression at eccentricities of 60 degrees and shift back along the horizontal meridian towards the area centralis. In two further animals, the fourth representation is located on the tentorial surface of the postlateral gyrus. One case is shown in Fig. 13*B*: here the receptive fields reverse their progression in the far periphery of the upper hemifield and shift back towards the horizontal meridian and the area centralis. The area is indicated in the map by the isoelevation lines +30, +20 and +10, just anterior from the posterior end of the splenial sulcus. The retinotopic arrangement of V2 and V3 in this latter case differs in only minor aspects from that of Fig. 12*A*:


A
LAT 15
LAT 7
pSpS
+40
+50
+30
+20
+15
+10
pPLGp
pPLGa
PLSp
pSSG
PLSa
+2
← POST 7
0
−2
← POST 1
mSSG
LS
ILG
2 mm
B
LAT 15
LAT 8
+50
+40
+30
+20
+10
pPLGp
aPLGp
PLSp
pSSG
mSSG
← POST 10
← POST 1
PLSa
IPLGa
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a part of the representation of the upper field periphery in V3 (on elevations +40 and +50) is located on the postlateral gyrus and not in the sulcus.

(4) Quantitative aspects of the representation of the visual field in V2 and V3

In order to know how much of the visual field is represented in the visual areas considered, the outer borders and the centres of the receptive fields located at the border of V2 were noted in the co-ordinate system of the visual field. The result is summarized for all animals in Fig. 14 (left). According to this plot, almost the entire visual field is represented in V2 taking the receptive field borders as the reference. A considerable part of the ipsilateral hemifield is represented too. In V2 as well as in the other areas this ipsilateral representation is formed by large fields the centres of which overlap the vertical meridian by not more than 5 degrees. The receptive fields in the periphery of V2 are also very large, if one considers the positions of the centres and the outer borders in the diagram of V2. Receptive fields in V1 are significantly smaller and their centres reach eccentricities of more than 80 degrees (Fig. 14, left, triangles). The plots for V3 (middle) and for the posterior reversal area (right) in Fig. 14 were made by marking the outer borders and the centres of receptive fields which were the first ones plotted after having left V2, or the last ones before visually unresponsive cortex was entered. Therefore, the plots do not represent the entire area of the visual field in the respective areas, because the fields located at the border between V2 and V3 or between V2 and posterior reversal theoretically are shared by either area. Only at two sites the representation is incomplete in V2 and V3. The periphery of the lower visual field just below the horizontal meridian was not found in V2 and in V3. This might be due to a small magnification at this place (see Discussion). Secondly the upper visual field seems to be incompletely represented in V3 since receptive fields 30–60 degrees above the area centralis were detected in no case.

The magnification factors (mm cortex/degree visual angle, see Daniel & Whitteridge, 1961) were calculated in the following way. The distance on the cortex between the representation of

Fig. 12. Maps of the representation of the area centralis, of the horizontal meridian and of the upper hemifield in V2 and V3. *A*, the map is constructed on the basis of 113 receptive fields. In the upper field the majority of isoazimuth lines runs parallel to the vertical meridian (isoazimuth zero, running across the postlateral gyrus). Posterior to it the azimuths 5 and 10 form part of V1; anterior to it the azimuths 5–75 form V2 and V3. The azimuths 5–50 run across the bottom of the postlateral sulcus, and on the anterior bank of the sulcus they turn first to anterior and then to lateral. The azimuths 65 and 75 are located on the posterior bank of the sulcus, at the lateral end of the representation. As can be seen, the isoelevations run generally perpendicularly to the isoazimuths. There are two lines for each of the elevations +10, +20 and +30. The posteriorly located ones (in V2) run across the postlateral gyrus and on the posterior bank of the sulcus they turn sharply to anterior and then to lateral. The elevations +40 and +50 are located posterolateral to +30. The anteriorly located ones (in V3) run across the posterior edge of the suprasylvian gyrus, into the postlateral gyrus. *B*, the visual field map is constructed on the basis of 170 receptive fields.

The cortical area explored (small dots) and the approximate location of the periphery of the horizontal meridian (one dark point in *A*, two dark points in *B*) are indicated on surface view of a right hemisphere. In *B* receptive fields representing identical parts of the periphery of the horizontal meridian in V2 are recorded from two cortical sites. Further explanations see legend to Figs. 2 and 4.

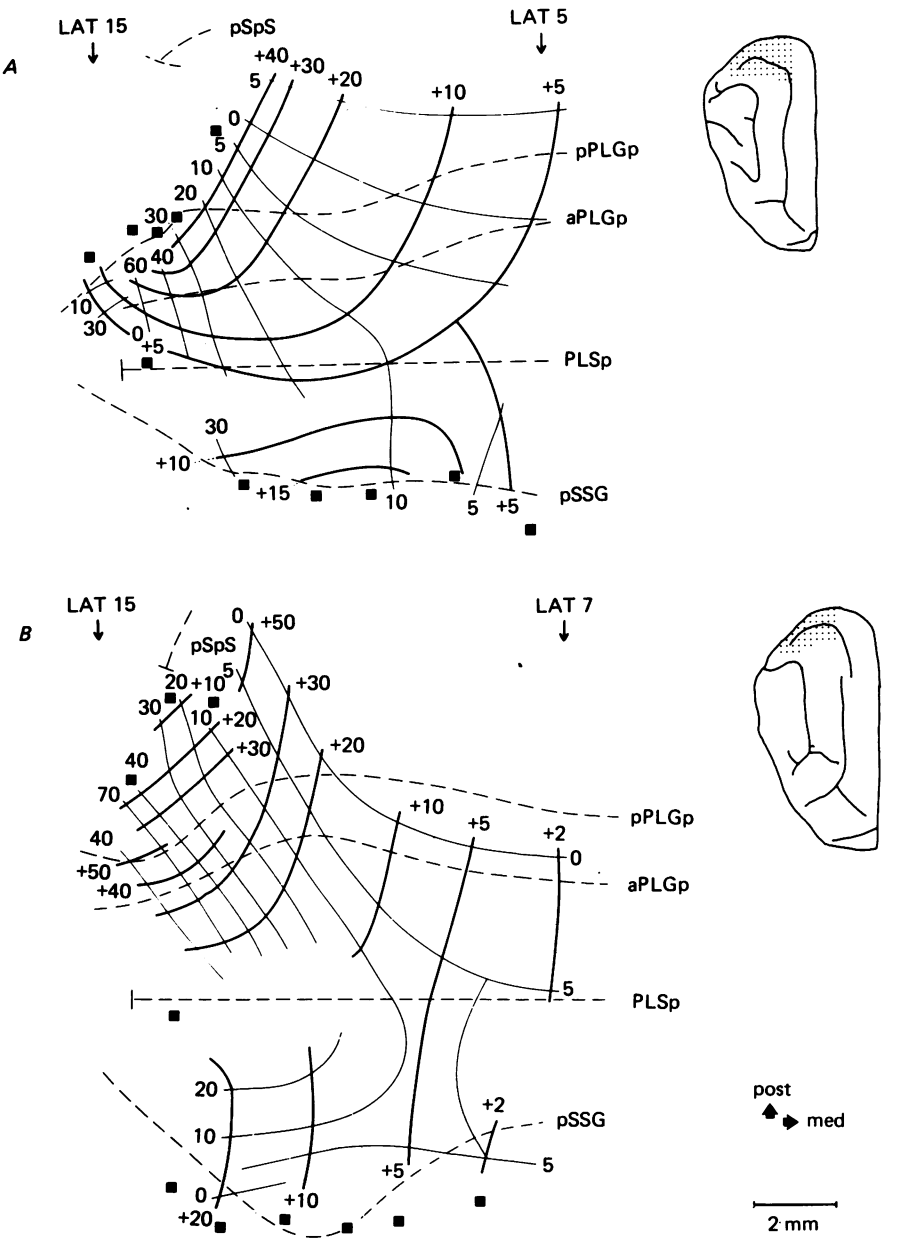

Fig. 13. Maps of the representation of the upper hemifield in V2 and V3. In *A*, the posterior portion of the postlateral sulcus was explored between 5 and 15 mm lateral the mid line and the map is contructed on the basis of 134 receptive fields. In *B*, the sulcus was explored between 7 and 15 mm lateral the mid line; the map was constructed on the basis of 151 receptive fields. The cortical area explored is indicated on surface views of a right hemisphere by small dots. Further explanations see legend to Figs. 2 and 4.

the area centralis and a recording site was plotted against the distance in the visual field between the area centralis and the receptive field centre for that recording site. Cortical distances were measured on the position maps, and visual field distances on the perimeter plots. Separate measurements were made along the various meridians of the visual field (Fig. 1*C*). The plots of cortical distance against visual field distance along each meridian were fitted by a line. From these curves magnification factors were calculated for various eccentricities. For comparison magnification factors in V1 were also determined. (The magnification factors along the vertical meridian at the borders between V1 and V2 are measured on the basis of receptive fields in V1 and in V2. When the magnification functions along the vertical meridian were calculated separately for V1 and V2, a difference was not found. This becomes also evident from the fact that the distances between isoelevation lines are about the same in V1 and V2 when measured adjacently to the vertical meridian.)

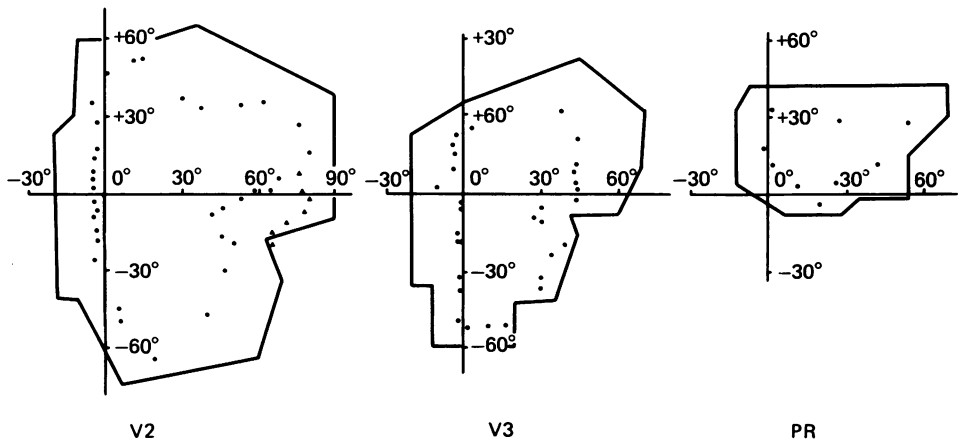

Fig. 14. Area of the visual field represented in V2, V3 and the posterior reversal area. The most peripheral receptive fields are indicated by their outer borders (continuous lines) and by their centres (points). In the diagram for V2 in addition the centres of the most peripheral receptive fields on the horizontal meridian in V1 are indicated by filled triangles. Further explanations see text.

The results are shown in Fig. 15. The area centralis has a much larger representation than the periphery of the visual field in all three areas. The cortical volume occupied by the representation of the area centralis, however, decreases from V1 to V2 to V3. The respective magnification factors (log M^2 measured at an eccentricity of 0·5 degrees) are 0·5–0·8 in V1 (Fig. 15*A*, *B*), 0·2–0·5 in V2 (Fig. 15*C*) and 0·1–0·2 in V3 (Fig. 15*D*). Significant differences between the magnification factors along the various meridians are seen in V1 as well as in V2 and V3. In V1 the magnification decreases from the lower hemifield to the horizontal meridian to the upper hemifield. The differences are significant from 10 degrees eccentricity on. In the central 5 degrees all parts of the field are nearly equally represented; only at the horizontal meridian a slightly higher magnification is measured (Fig. 15*A*). In V2 the magnification along the lower vertical meridian is considerably higher than that along the upper vertical meridian. In contrast to V1, however, there is no difference in V2 (Fig. 15*C*) between the magnification factors along the lower and upper oblique meridian. They both are from 10 degrees eccentricity on of the same order as the magnifications along the upper vertical meridian at the V1/V2 border (Fig. 15*A*). In further contrast

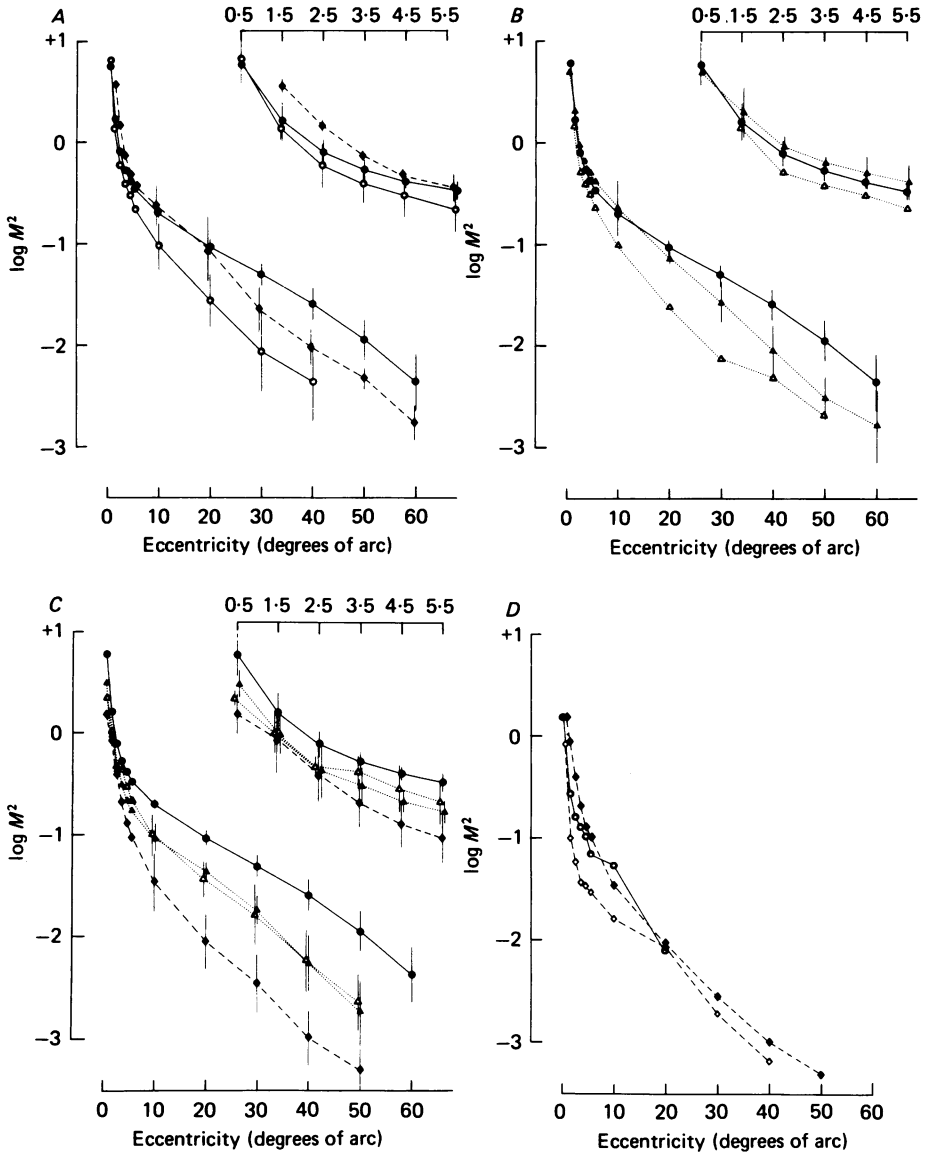

Fig. 15. Magnification factors in V1, V2 and V3 as a function of eccentricity. In three diagrams the magnification factors for the central 5 degrees of the representation of the visual field are shown also on a magnified abscissa (upper right in *A*, *B* and *C*). *A*, magnification in V1 along the lower vertical meridian (●— —●), the upper vertical meridian (○——○) and the horizontal meridian (◆- -◆). *B*, magnification in V1 along the upper oblique meridian (△ . . . △) and the lower oblique meridian (▲ . . . ▲). For comparison the lower vertical meridian is given (●——●). *C*, magnification in V2 along the upper oblique meridian (△ . . . △), the lower oblique meridian (▲ . . . ▲) and the horizontal meridian (◆- -◆). For comparison the lower vertical meridian (●——●) in V1 is given. *D*, magnification in V3 along the upper vertical meridian (○——○) and the horizontal meridian (◇– –◇). For comparison the horizontal meridian in V2 is given (◆- -◆). Means and S.D.s were calculated from at least four animals. Means without S.D.s were calculated from two animals (V3) or represent the result from one animal (V1, upper oblique meridian). For calculation of the magnification along the vertical meridian in V1 and V2 see text.

to V1, in V2 the smallest magnification is measured along the representation of the horizontal meridian. Here the magnification drops from 5 to 10 degrees eccentricity, significantly below the values measured along the other meridians. The magnification functions in V3 were determined for the upper vertical meridian and the horizontal meridian only (Fig. 15*D*). The values were equal to or even smaller than the magnification along the horizontal meridian in V2. At the other meridians in V3 the number of receptive fields in each animal was too small for a reliable calculation.

DISCUSSION

The retinotopy of V2 and V3

The basic features of the representation of the visual field in V2 and V3 are summarized in Fig. 16. The map reveals the two characteristic features in the retinotopic arrangement of V2 and V3, which make these areas so different from V1 (Woolsey, 1971; Tusa *et al.* 1978). The border between V2 and V3 on the lateral gyrus is formed by the periphery of the lower hemifield, and in the postlateral sulcus by an imaginary line running along the horizontal meridian about 5–10 degrees in the upper hemifield. A similar retinotopy has also been suggested by Tusa (1975). It appears as if this arrangement is caused by a split across the representation of the visual hemifield slightly above the horizontal meridian. The split begins at an eccentricity of approximately 10 degrees and actually divides the representation of the visual field in two parts. One part contains the lower hemifield and the horizontal meridian, the other part contains most of the upper hemifield, and sometimes also parts of the horizontal meridian. In the cortex the border of one part runs across the anterior portion of the postlateral sulcus, the border of the other part runs along the bottom of the posterior portion of the postlateral sulcus. Thus adjacent parts of the visual field are represented in V2 and V3 at sites which are some mm distant from each other. The areas and sometimes even the centres of receptive fields recorded at the edges of both parts occupy identical parts of the visual field.

Another special feature of the retinotopy in V2 and V3 is the 'island' like representation of the periphery of the lower hemifield and of the horizontal meridian. This type of representation has recently been reported by Donaldson & Whitteridge (1977). We confirm here their findings and show that the islands are constant features of the representation of the visual field in V2 and V3. We also demonstrate that they are confined to the lower hemifield and the horizontal meridian. According to the retinotopic arrangement at the V2/V3 border discontinuities are introduced into the representation of the visual field. The principle of these is that the visual field periphery is represented in several patches, the cortical space in between the patches being filled by parts of the visual field closer to the vertical meridian. The number of the patches is three or four depending on whether the lower field periphery is represented in one or two islands.

The retinotopic arrangement at the outer border of V2 in other animals is different from that in the cat. In rodents (Thompson, Woolsey & Talbot, 1950; Adams & Forrester, 1968; Hughes, 1971; Dräger, 1975) V2 is a mirror image of V1. In monkeys V2, the representation of the horizontal meridian is split into two branches which

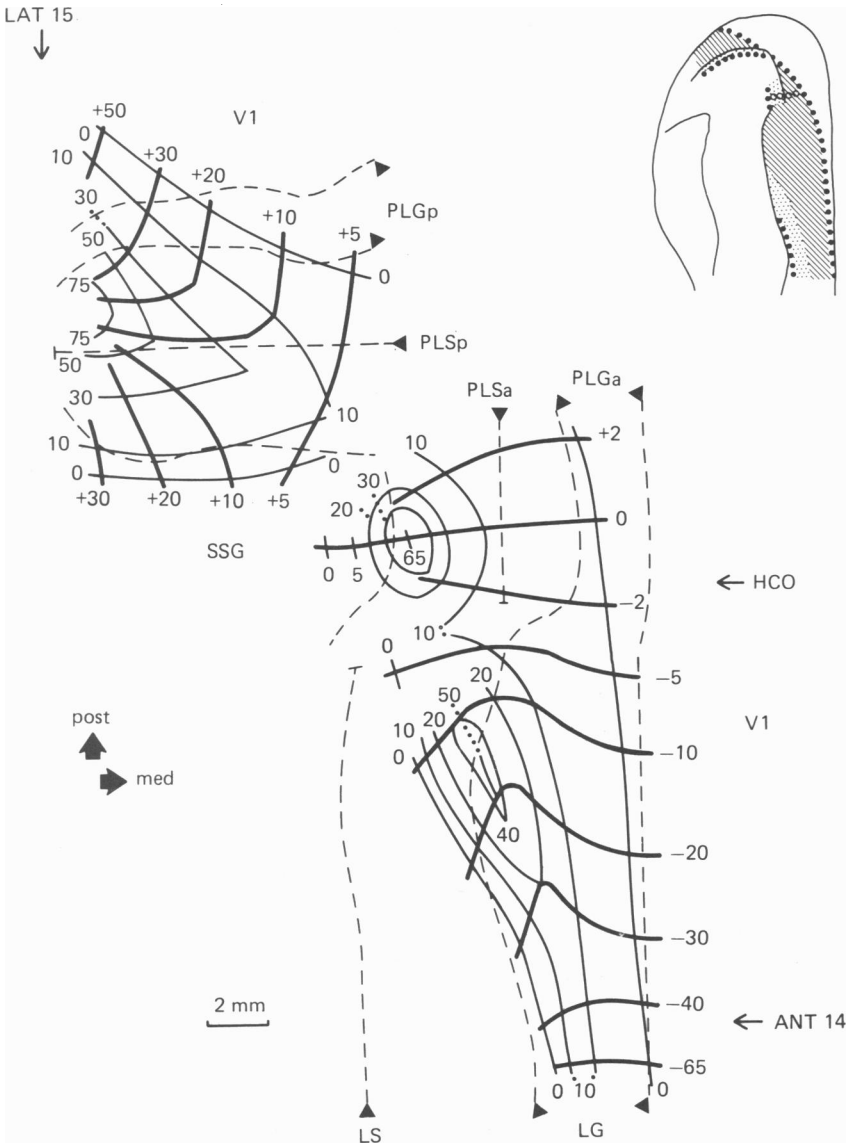

Fig. 16. Basis retinotopy of V2 and V3 in the cat. The map has been prepared from two animals, and is projected upon the extended surface of a right hemisphere. HCO, Interaural plane of the Horsley–Clarke co-ordinate system; ANT 14, frontal plane 14 mm anterior the interaural plane HCO; LAT 15, parasagittal plane 15 mm lateral from the mid line of the brain. The first visual area (V1) is located medial and posterior from V2. Most of the representation of the upper hemifield in V2, and in V3 is hidden in the posterior portion of the postlateral sulcus as can be seen from the surface view (upper right). A part of the representation of the vertical meridian in V3 is visible on the lateral gyrus and on the medial and the posterior edge of the suprasylvian gyrus. Filled circles: representation of the vertical meridian in V1/V2 and in V3. Open circles: representation of the horizontal meridian in V2 and V3. Striped area, V2; dotted area, V3.

form the outer border of the lower and upper field, respectively (Allman & Kaas, 1974; Zeki, 1969, 1977; van Essen & Zeki, 1978). In the owl monkey, the split begins 5–10 degrees distant from the area centralis (Allman & Kaas, 1974) and in the rhesus monkey it starts at an eccentricity of 1 degree (van Essen & Zeki, 1978).

It is clear from the results that the map shown in Fig. 16 is representative only for some cats. In the majority of the animals this simple and basic map is modified to a greater or lesser extent. Major modifications concerned the locations of the area centralis in V1/V2 and in V3, and the location of the periphery of the horizontal meridian in V2/V3. Reasons for the displacement of these various visual field points within the maps are not known; neither rotations or mediolateral displacements of the maps with respect to the anteroposterior axis of the brain (Whitteridge, 1973; Tusa *et al.* 1978) can explain them. Likewise variations of the visual field points with respect to the interaural plane of the Horsley–Clarke co-ordinate system cannot be explained by interindividual variations in the location of the interaural plane itself (see also Tusa *et al.* 1978).

We have made careful controls in order to rule out experimental errors. During the experiments we controlled for movements and rotations of the eyes. As an additional control as many as possible receptive fields especially on the vertical meridian and in the visual field periphery were plotted for both eyes. This allows one to estimate reliably the relative position of the eyes to each other, and also the eye position with respect to the co-ordinates of the perimeter. On the basis of these controls our findings on the interindividual variability in the retinotopic arrangement certainly are independent from movement of the eyes. It has been shown recently that interindividual variability in the topographical arrangement of a central map is not confined to the visual areas. Significant variations have been reported for the anterior auditory field in the cat (Knight, 1977) and for the sensory areas in SI of the monkey (Merzenich, Kaas, Sur & Lin, 1978).

The area of the visual field represented in V2 and V3

Earlier investigators have claimed that only a limited part of the visual field is represented in V2 and V3 (Bilge *et al.* 1967; Woolsey, 1971; Tusa, Palmer & Rosenquist, 1975; Whitteridge, 1973). The most peripheral receptive fields reported were located at 40–45 degrees eccentricity.

By contrast we have found in some animals that nearly the entire hemifield is represented in V2 as well as in V3. The differences between the two sets of findings might be attributed to two facts. First, the small cortical volume devoted to the far periphery in V2 and V3 is difficult to detect in experiments when the cortical activity is sampled at intervals of not less than 200 μm. Recently, for example, we have found that in some animals the lower hemifield in V2 and V3 is represented out to 75 degrees. In these experiments unit activity was sampled in steps of less than 30 μm (K. Albus and R. Beckmann, unpublished observation). Secondly, the differences might be attributed to the interindividual variations in the extent of the visual field represented in V2 and V3 as we have found them.

We wondered whether incomplete representations were caused by the depressant effects of barbiturates, which were used during the initial experiments. Some experiments were performed under N_2O/O_2 anaesthesia which was supplemented by low

doses of pentobarbitone (see Methods). Under these conditions a third representation of the upper hemifield was found in one animal and in two others the third representation was incomplete. A significant effect of the anaesthetic regimen on our results can therefore be excluded.

The non-linear representation of the retina in the visual cortex

We have found that the magnification factors become progressively smaller from V1 to V2 to V3. The cortical volume occupied by one representation decreases from V1 to V2 to V3. The cat therefore is different from the rhesus monkey in which the magnification in central parts of the representation in V2 is about the same as in V1 (van Essen & Zeki, 1978). A further difference between cat and rhesus monkey is that in the latter the magnification functions in V1 along the various meridians are equal (Daniel & Whitteridge, 1961), whereas in the former they are not equal. In V1 of the cat, in the central 5 degrees the magnification along the horizontal meridian is slightly higher than along the other meridians. In paracentral and peripheral parts of the representation, however, the magnification is highest along the lower vertical meridian, and it diminishes progressively from the lower hemifield to the horizontal meridian to the upper hemifield and finally to the upper vertical meridian. In V2 there is no difference between lower and upper hemifield and the smallest magnification is measured along the horizontal meridian. These findings make it questionable whether cortical magnification can be explained solely on the basis of ganglion cell densities in the retina. According to such density plots (Stone, 1965; Hughes, 1975) one would expect the highest density to occur along the entire horizontal meridian and not only along its central five degrees, as we have found it. The overrepresentation of the lower vertical meridian might be partly due to the fact that the upper retina contains more ganglion cells than the lower retina (Hughes, 1975). There must exist, however, other factors which determine the cortical organization of the representations of the retina. A central factor is very likely to be involved in how the horizontal meridian is represented in V2. We have shown that the representation of the visual field in V2 is split into two sectors. Receptive fields recorded at the edges of the sectors occupy the same area in the visual field. Accordingly, one area in the visual field is represented twice in V2 and in V3. One would then expect that the magnification measured along one of those half-representations would be smaller than when measured along an undivided representation of the horizontal meridian. This is what we have actually found.

The cortical location of the maps

We found a close relationship between area 18, as defined by cyto- and myeloarchitectonic criteria, and V2, as defined electrophysiologically. It was, however, difficult to relate V3 with area 19, since the latter area is not easily differentiated from laterally adjacent areas on the basis of anatomical criteria. Our results on the location of V2 agree with the location of the paravisual area (paV) given by Sanides & Hoffmann (1969); they disagree with the results of Heath & Jones (1971) and Otsuka & Hassler (1962) according to which area 18 ends in the postlateral sulcus. Interestingly Otsuka & Hassler (1962) have noted that area 18 may extend across the postlateral sulcus onto its anterior bank as we have found it in two animals. In no case

did V2 extend into the posterior splenial sulcus as it has been indicated for area 18 by Gurewitsch & Chatschaturian (1928). According to our findings, the upper field representation in V3 hardly spreads across the posterior edge of the suprasylvian gyrus to anterior. This disagrees with the results of Sanides & Hoffmann (1969) and of Heath & Jones (1971).

The representation of the lower field in V2 and V3 and the respective parts of areas 18 and 19 coincide roughly. According to our results only the medial part of the paravisual area (paVm, Sanides & Hoffmann, 1969) is visually active. It remains unclear to what region the fourth representation belongs. It is certainly not part of area 19. It is also not part of the splenial area (Kalia & Whitteridge, 1973), since it is clearly outside the splenial sulcus. Interestingly, Sanides & Hoffmann (1969) have described a small lateroposterior paravisual area, just dorsal from the posterior end of splenial sulcus. This area shows a limbic pattern of myelinization and cortical layering.

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REFERENCES

ADAMS, D. A. & FORRESTER, J. M. (1968). The projection of the rat's visual field on the cerebral cortex. *Q. Jl exp. Physiol.* **53**, 327–336.

ALBUS, K. & BECKMANN, R. (1978). Interindividual variability in the arrangement of visual field maps in the second and third visual area in the cat. *Pflügers Arch. Eur. J. Physiol. Suppl.* **337**, *R* **83**, 303.

ALLMAN, J. M. & KAAS, J. H. (1974). The organization of the second visual area (V2) in the owl monkey: a second order transformation of the visual hemifield. *Brain Res.* **76**, 247–265.

ALLMAN, J. M. & KAAS, J. H. (1975). The dorsomedial cortical visual area: a third tier area in the occipital lobe of the owl monkey (*Aotus trivirgatus*). *Brain Res.* **100**, 473–487.

ALLMAN, J. M. & KAAS, J. H. (1976). Representation of the visual field on the medial wall of occipital-parietal cortex in the owl monkey. *Science, N.Y.* **191**, 572–575.

BECKMANN, R. & ALBUS, K. (1977). The retinotopic organization of the second visual area (V2) in the cat. *Pflügers Arch. Eur. J. Physiol. Suppl.* **368**, *R* **42**, 168.

BILGE, M., BINGLE, A., SENEVIRATNE, K. N. & WHITTERIDGE, D. (1967). A map of the visual cortex in the cat. *J. Physiol.* **191**, 116–118*P*.

BISHOP, P. O., KOZAK, W. & VAKKUR, G. J. (1962). Some quantitative aspects of the cat's eye: axis and plane of reference, visual field co-ordinates and optics. *J. Physiol.* **163**, 466–502.

DANIEL, P. & WHITTERIDGE, D. (1961). The representation of the visual field on the cerebral cortex in monkeys. *J. Physiol.* **159**, 203–221.

DONALDSON, I. M. L. & WHITTERIDGE, D. (1977). The nature of the boundary between cortical visual areas II and III in the cat. *Proc. R. Soc.* B **199**, 445–462.

DRÄGER, U. C. (1975). Receptive fields of single cells and topography in mouse visual cortex. *J. comp. Neurol.* **160**, 269–290.

ESSEN, VAN D. C. & ZEKI, S. M. (1978). The topographic organization of the rhesus monkey prestriate cortex. *J. Physiol.* **277**, 193–226.

GUREWITSCH, M. & CHATSCHATURIAN, A. (1928). Zur Cytoarchitektonik der Grosshirnrinde der Feliden. *Z. Anat. EntwGesch.* **87**, 100–138.

HEATH, C. J. & JONES, E. G. (1971). The anatomical organization of the suprasylvian gyrus of the cat. *Ergebn. Anat. EntwGesch.* **45**, 1–64.

HUBEL, D. H. & WIESEL, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* **160**, 106–154.

HUBEL, D. H. & WIESEL, T. N. (1965). Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat. *J. Neurophysiol.* **28**, 229–289.

HUGHES, A. (1971). Topographical relationships between the anatomy and the physiology of the rabbit visual system. *Documenta Ophth.* **30**, 33–159.

HUGHES, A. (1975). A quantitative analysis of the cat's retinal ganglion cell topography. *J. comp. Neurol.* **163**, 107–128.

KALIA, M. & WHITTERIDGE, D. (1973). The visual area in the splenial sulcus of the cat. *J. Physiol.* **232**, 275–283.

KNIGHT, P. L. (1977). Representation of the cochlea within the anterior auditory field (AAF) of the cat. *Brain Res.* **130**, 447–467.

MERZENICH, M. M., KAAS, J. H., SUR, M. & LIN, S. S. (1978). Double representation of the body surface within cytoarchitectonic areas 3b and 1 in SI in the owl monkey (*Aotus trivirgatus*). *J. comp. Neurol.* **181**, 41–74.

NIKARA, T., BISHOP, P. O. & PETTIGREW, J. D. (1968). Analysis of retinal correspondence by studying receptive fields of binocular single units in cat's striate cortex. *Exp. Brain Res.* **6**, 353–372.

OTSUKA, R. & HASSLER, R. (1962). Über Aufbau und Gliederung der corticalen Sehsphäre bei der Katze. *Arch. Psychiat. Nerv.-Krankh.* **203**, 212–234.

PALMER, L. A., ROSENQUIST, A. C. & TUSA, R. J. (1978). The retinotopic organization of lateral suprasylvian visual areas in the cat. *J. comp. Neurol.* **177**, 237–256.

SANIDES, F. & HOFFMANN, J. (1969). Cyto- and myeloarchitecture of the visual cortex of the cat and of the surrounding integration cortices. *J. Hirnforsch.* **11**, 79–104.

STONE, J. (1965). A quantitative analysis of the distribution of ganglion cells in the cat's retina. *J. comp. Neurol.* **124**, 337–352.

SPRAGUE, J. M., LEVY, J., DIBERARDINO, A. & BERLUCCHI, G. (1977). Visual cortical areas mediating from discrimination in the cat. *J. comp. Neurol.* **172**, 441–488.

THOMPSON, J. A., WOOLSEY, C. N. & TALBOT, S. A. (1950). Visual areas I and II of cerebral cortex of rabbit. *J. Neurophysiol.* **13**, 227–289.

TUSA, R. J. (1975). The retinotopic organization of V1, V2 and V3 in the cat. *Anat. Rec.* **181**, 497.

TUSA, R. J., PALMER, L. A. & ROSENQUIST, A. C. (1975). The retinotopic organization of the visual cortex in the cat. *Soc. Neurosci. Abstr.* **1**, 52.

TUSA, R. J., PALMER, L. A. & ROSENQUIST, A. C. (1978). The retinotopic organization of area 17 (striate cortex) in the cat. *J. comp. Neurol.* **177**, 107–128.

WHITTERIDGE, D. (1973). Projection of the optic pathway to the visual cortex. In *Handbook of Sensory Physiology*, ed. JUNG, R., vol. VII/3B, pp. 247–268. Berlin: Springer Verlag.

WOOLSEY, C. N., DAUBE, J. P., HOFFMANN, J., KAAS, J. H. & LADPLI, S. (1967). Representation of the visual field in visual areas I and II of the cat's cerebral cortex. *Fedn Proc.* **26**, 656.

WOOLSEY, C. N. (1971). Comparative studies on cortical representation of vision. *Vision Res.*, Suppl. no. **3**, 365–382.

ZEKI, S. M. (1969). Representation of central visual fields in prestriate cortex of monkey. *Brain Res.* **14**, 271–291.

ZEKI, S. M. (1975). The functional projections from striate to prestriate visual cortex in the rhesus monkey. *Cold Spring Harb. Symp. quant. Biol.* **40**, 591–600.

ZEKI, S. M. (1977). Simultaneous anatomical demonstration of the representation of the vertical and horizontal meridians in areas V2 and V3 of rhesus monkey visual cortex. *Proc. R. Soc.* B **195**, 517–523.

ZEKI, S. M. (1978). Uniformity and Diversity of structure and function in rhesus monkey prestriate visual cortex. *J. Physiol.* **277**, 273–290.