Brain Research, 76 (1974) 247–265

THE ORGANIZATION OF THE SECOND VISUAL AREA (V II) IN THE OWL MONKEY: A SECOND ORDER TRANSFORMATION OF THE VISUAL HEMIFIELD

J. M. ALLMAN* AND J. H. KAAS*

Laboratory of Neurophysiology, University of Wisconsin, Madison, Wisc. 53706 (U.S.A.)

(Accepted March 4th, 1974)

SUMMARY

The visuotopic organization of the second visual area (V II) in the owl monkey was mapped by determining the receptive field positions for single neurons and small clusters of neurons recorded with microelectrodes. Our data indicate that V II is a long narrow strip of cortex which appears to correspond to area 18 of Brodmann[8]. The results also indicate that the topological transformation of the visual field in V II is fundamentally different from that in the primary visual area (V I). In V I, adjacent loci in the contralateral half of the visual field are always represented in adjacent cortical loci, and thus V I is a simple topological representation which we refer to as a *first order transformation* of the visual hemifield. In contrast, adjacent loci in the contralateral hemifield are *not* always represented in adjacent loci in V II. Beyond the central 7° in V II, the representation of the horizontal meridian *splits* to form most of the anterior border of V II, and the upper and lower quadrants of the visual field are represented separately. Thus, two adjoining parts of the visual field on each side of the horizontal meridian can be represented in quite separate parts of V II. We refer to V II as a *second order transformation* of the visual hemifield and suggest that V II serves as a functional adjunct to V I.

INTRODUCTION

The existence of a second visual area adjoining the primary visual area, striate cortex, was postulated by early investigators such as Brodmann[8], Campbell[9] and Elliot Smith[22] on the bases of architectonic structure and clinical observations. However, evidence of a second systematic representation of the visual field next to the

* Present address: Department of Psychology, Vanderbilt University, Nashville, Tenn. 37240, U.S.A.

representation in striate cortex was first discovered by Talbot[25] in electrophysiological mapping experiments in the cat. The organization of this second visual area, later termed V II by Woolsey and Fairman[31], has been most completely explored in the rabbit[17,26,32] and to a lesser extent in the cat[7,15,30] and several other mammals[13,19,20], but the organization of V II in primates is not well known[2,10]. In our previous report[2] on the organization of striate cortex (V I) and the immediately adjoining cortex in the owl monkey, we demonstrated that V II adjoins approximately 90% of the border of V I, but we did not attempt to fully explore V II. However, our preliminary data did indicate that the organization of V II in the owl monkey is not a simple mirror image of V I. Thus we sought to determine how the visual field is represented in V II of the owl monkey. A second goal was to determine to what extent V II corresponds to an architectonic field distinct from surrounding cortex.

In the experiments of this report, V II of the owl monkey was explored in detail, and the recording sites were related to cortical architectonics. As expected, our data indicate that V II is a long narrow strip of cortex which appears to correspond to area 18 of Brodmann[8]. However, the results also indicate that the topological transformation of the visual field in V II is fundamentally different from that in V I. In V I, adjacent loci in the contralateral half of the visual field are always represented in adjacent cortical loci, and thus V I is a simple topological representation, which we refer to as a *first order transformation* of the visual hemifield. In contrast, adjacent loci in the contralateral hemifield are *not* always represented in adjacent loci in V II. Beyond the central 7° in V II, the representation of the horizontal meridian splits to form most of the anterior border of V II, and the upper and lower quadrants of the visual field are represented separately. Thus, two adjoining parts of the visual field on each side of the horizontal meridian can be represented in quite separate parts of V II. We refer to V II as a *second order transformation* of the visual hemifield. Both first and second order transformations are found in other visual areas of the owl monkey[1,4,6].

METHODS

The experimental procedures have been described previously[1]. The visuotopic organization of V II was explored extensively with electrophysiological mapping methods in 6 owl monkeys (*Aotus trivirgatus*). More limited explorations were done in a number of other owl monkeys. The monkeys were anesthetized with urethane and prepared for recording. Microelectrodes were used to record from small clusters of neurons or occasionally from single neurons in visual cortex. Receptive fields were determined by moving slits of light or bars of shadow on the surface of a translucent plastic hemisphere centered in front of the contralateral eye. The ipsilateral eye was covered by an opaque shield and was not stimulated. After recording, the animals were perfused with formol-saline, and the brains were removed, dehydrated, embedded in celloidin, and alternate series of 30 μm sections were stained with thionin for cell bodies or hematoxylin for myelin (Heidenhain–Woelcke technique). Electrode tracts and recording sites were located in the histological sections and related to receptive fields.

RESULTS

The second visual area is a long narrow belt adjoining 90% of the border of striate cortex in the owl monkey[2]. Because of the shape of V II, the area is difficult to explore completely with microelectrodes in individual experiments. Therefore, results from different parts of V II from several experimental animals are discussed below.

All recording sites with receptive fields belonging to a single second systematic representation of the visual field were considered to be within V II. Some receptive fields for recording sites within V I are also included in this report to indicate how clearly two separate types of cortical organization appear. Receptive fields for recording sites immediately anterior to V II, in the region usually considered to be V III or area 19, were found to belong to a number of additional representations of the visual field, the particular representation depending on which region of bordering cortex was explored. As with the V I–V II distinction, changes in organization at the anterior border of V II were also clearly apparent (see, for example, ref. 1, Fig. 8). Since each of these additional visual areas deserves a full description, receptive fields for recording sites anterior to V II will be published elsewhere. Brief reports on two of these areas are available[4,6].

As is clearly apparent from Figs. 1–3, the receptive fields for V II were larger than similarly located receptive fields for V I. It was usually more difficult to activate neurons in V II than in V I.

The dorsal surface

Because of its accessibility, the dorsal surface of visual cortex was the most fully explored. Previously, we had illustrated receptive fields for recording sites in V II of the dorsal surface of the owl monkey[1,2] and of a prosimian, *Galago senegalensis*[3]. Likewise, Cowey[10] has illustrated receptive fields for recordings in V II of the dorsal surface of the squirrel monkey. In addition, the overall visuotopic organization of V II of the dorsal surface of the squirrel monkey can be predicted from the pattern of degeneration in this region after small lesions in different parts of the dorsally accessible striate cortex[23,24], if one assumes that similar parts of the representation in each area are connected. These earlier observations are consistent with the conclusions based on the more extensive results of the present report.

The basic organization of V II of the dorsal surface is apparent when receptive field locations are related to recording sites in Fig. 1 where 4 posterior to anterior rows of recording sites extend from V I across V II. As has been noted previously for primates[2,10,16], there is a reversal of visuotopic organization in V II as compared to V I. Thus in row 1, the first two recording sites, A and B, are in V I, and the receptive field for recording site B, near the V I–V II border, is nearer the vertical meridian of the visual field than the receptive field for the more posterior recording site A. The receptive fields for the progression of recording sites across V II, C through G, reverse the trend toward the vertical meridian and move away toward temporal periphery of the visual field. Similar reversals can be noted in each of the 4 progressions, and this reversal of organization is basic to the second visual area. However, it is important

to note two other aspects of the data. First, each row of receptive fields extends only part way into the contralateral hemifield. The more medial progressions extend further temporally in the visual field than the lateral rows, but none extend to the extreme temporal periphery, which is clearly not represented in V II of the dorsal surface. Only a restricted part of the horizontal dimension of the visual field is represented across the rostrocaudal width of V II of the dorsal surface. In contrast, a single strip of cortex from the border of V I on the dorsal surface to the border of V I folded into the calcarine sulcus can represent the complete horizontal dimension from the vertical meridian to the temporal periphery[2]. Second, the receptive fields for the most anterior recording sites in Fig. 1 are overlapping or close to the horizontal meridian, and we conclude that the anterior border of V II on the dorsal surface is formed by a representation of the horizontal meridian. Again, V II differs from V I in that no border in V I corresponds to the horizontal meridian. Thus, V II of the owl monkey is characterized by a reversal of the organization seen in V I, but the organization is fundamentally different, and V II is not simply a 'mirror image' of V I.

As demonstrated in Fig. 1, the second visual area of the dorsal surface represents the part of the lower visual field just below the horizontal meridian. The receptive fields lowest in the visual field correspond to the most medial and posterior recording sites in the illustration. Receptive fields nearer the horizontal meridian are for recording sites more lateral or anterior. As previously illustrated (see ref. 1, Fig. 8), receptive fields for all recording sites near the most lateral part of the dorsal surface (*i.e.*, the lateral surface), are along the horizontal meridian. The receptive fields for neurons at the anterior border of V II at this location are only about 7° from the vertical meridian. Thus, we conclude that the representation of the horizontal meridian starts at the center of gaze at the V I–V II border, extends across the width of V II encompassing about the central 7° of visual field, and turns at right angles to form the anterior border of the lower field representation on the dorsal surface. We shall see that the horizontal meridian also forms the anterior border of V II of the upper field representation, and in that sense splits to form the border in two directions after crossing the width of V II.

The upper medial wall and upper bank of the calcarine sulcus

As shown above, the more central part of the lower visual quadrant is represented on the dorsal surface. The rest of the lower visual quadrant is represented in the part of V II that occupies the medial wall and the most medial part of the upper bank of the calcarine sulcus. Previously, we showed receptive fields for recording sites along vertical electrode tracts extending from the dorsal surface through cortex of the medial wall including both V I and V II (see ref. 2, Fig. 3). Receptive fields for recording sites near the V I–V II border were along the vertical meridian between 20° and 30° in the lower visual field. As on the dorsal surface, receptive fields for recording sites nearer the anterior border of V II were more temporal in the visual field and were nearer the horizontal meridian.

Recordings from the belt-like second visual area just as it curves onto the upper bank of the calcarine sulcus from the medial wall are shown in Fig. 2 in a parasagittal brain section. Because the receptive fields for any column of cells perpendicular to

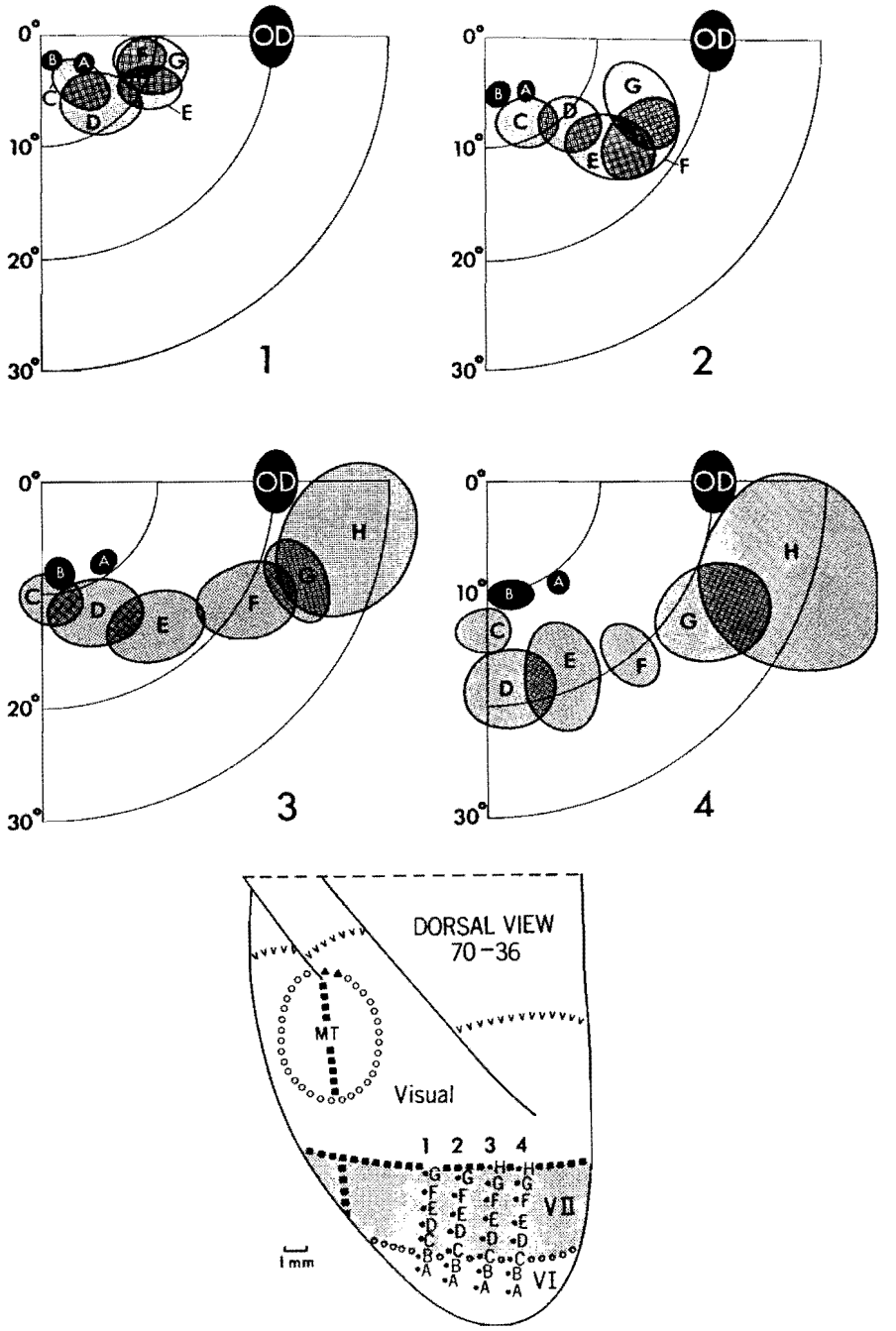

Fig. 1. Receptive fields for recording sites in V I and V II on the dorsal surface of the occipital lobe of owl monkey 70-36. The center diagram in the bottom row is a drawing of the posterior half of the left cerebral hemisphere. In this drawing the posterior pole of the hemisphere is at the bottom and the medial edge is on the right. In each of the 4 vertical rows in this drawing, recording sites A through G or H are indicated. The receptive fields for each of these 4 vertical rows are shown in perimeter charts 1–4, in which the central 30° of the lower right visual quadrant is displayed. The brain surface devoted to V II and the receptive fields mapped from V II are shaded. In the drawing of the brain, the small circles indicate the representation of the vertical meridian of the visual field; the black squares indicate the horizontal meridian of the contralateral half of the visual field; the black triangles indicate the extreme temporal periphery of the contralateral half of the visual field. The rows of VVVV indicate the anterior limits of visual cortex. The anterior limits of visual cortex and the location of the middle temporal visual area (MT) are based on data obtained from other experiments. The black oval marked 'OD' indicates the projection of the optic disc in the visual field.

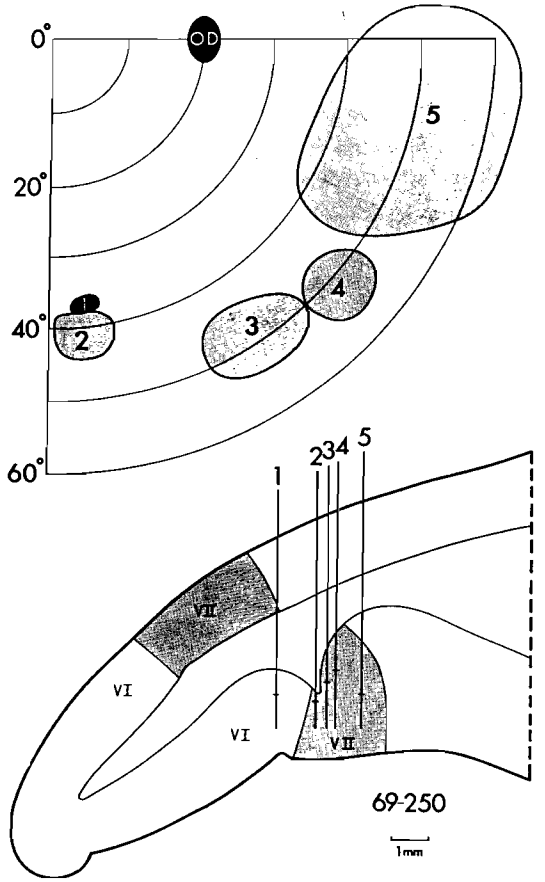

Fig. 2. Receptive fields for recording sites in V I and V II on the upper bank of the calcarine sulcus in the left occipital lobe of owl monkey 69-250. The lower diagram is a drawing of a parasagittal section through the occipital lobe. Anterior is to the right. Microelectrode penetrations are indicated by numbered vertical lines, and recording sites are marked by horizontal bars across these lines. The receptive fields corresponding to these recording sites are shown in the perimeter chart which displays the central 60° of the lower right visual quadrant.

the cortical surface are all similarly placed, these recording sites indicate the representation of the visual field at the cortical surface of the medial wall near the calcarine sulcus (see Fig. 4 for a cortical surface view of V II with superimposed visual field coordinates). The recording site nearest the V I–V II border in Fig. 2 relates to a receptive field near the vertical meridian about 40° into the lower visual quadrant (see also ref. 2, Fig. 8). The adjacent recording sites which form a progression toward the anterior border of V II correspond to a progression of receptive fields toward the temporal periphery and horizontal meridian of the visual field. The anterior border of V II near recording site 5 represents the horizontal meridian some 50° from the center of gaze. Thus the type of organization seen in V II of the dorsal surface is continued in V II of the medial bank, with the posterior border of V II corresponding to the vertical meridian and the anterior border to the horizontal meridian.

Only the most medial part of V I of the upper bank of the calcarine sulcus is

bordered by V II; the more lateral part of striate cortex of the upper bank represents the extreme temporal periphery of the visual field and is not bordered by V II[2]. In the present series of experiments, a few receptive fields were mapped from recording sites in the small portion of V II on the upper bank of the calcarine sulcus, and these results indicate that the more peripheral parts of the lower visual quadrant are represented in this end of the belt-like second visual area. In a like manner, the other end of V II, on the lower bank of the calcarine sulcus represents the more peripheral parts of the upper visual quadrant, as can be seen in Fig. 3. The representation of the temporal periphery of the visual field more than 60° from the center of gaze appears to occupy very little tissue in V II.

The ventral surface and the lower bank of the calcarine sulcus

The part of V II extending onto the ventral or tentorial surface and curving around to form part of the lower bank of the calcarine sulcus represents the upper visual quadrant. This is apparent in Fig. 3 where posterior to anterior rows of recording sites are located in V II of the tentorial surface and the lower bank of the calcarine sulcus; the corresponding receptive fields are in the upper visual quadrant. A number of receptive fields are also shown for V I of the tentorial and calcarine cortex (*cf.* Fig. 3 with ref. 2, Figs. 4 and 6). The part of the upper visual quadrant near gaze is represented laterally in V II of the tentorial surface near the border with V I. The most lateral row of recording sites in V I of the tentorial surface only includes about 15° of horizontal dimension of the visual field (receptive fields 17T, 18T and 19T) while the most medial row of recording sites, 2T, 3T, 4T, 6T and 7T, includes about 45° of horizontal dimension. The vertical meridian is represented along the V I border and more temporal parts of the upper visual quadrant are found anteriorly and medially. As for other parts of V II, the receptive fields near the anterior border of V II of the tentorial surface are near the horizontal meridian.

The cortex in the medial portion of the tentorial surface is continuous with the cortex on the lower bank of the calcarine sulcus. The receptive fields for the row of recording sites 4L through 7L are located higher in the visual field than the receptive fields for the recordings sites in the tentorial surface in the same penetrations. Proceeding anteriorly in row 4L through 7L, the receptive fields move from near the vertical meridian temporally in the visual field and approach the horizontal meridian about 40° from the center of gaze. Little cortex is devoted to the remaining more peripheral part of the upper visual quadrant, but more lateral recording sites from V II in the upper bank (14L and 24L) indicate that in this region the V I–V II border represents the vertical meridian of the extreme upper visual field. More anterior recording sites (15L and 16L) have receptive fields displaced from the vertical meridian, but these rather peripheral receptive fields are not close to the horizontal meridian.

The location and organization of V II: a summary

The location and organization of the second visual area in the owl monkey is shown in Fig. 4 where V II is illustrated as a band of cortex bordering most of V I and with visual field coordinates superimposed. The figure is based on combined experimental results. Data from recordings from different experiments in which limited

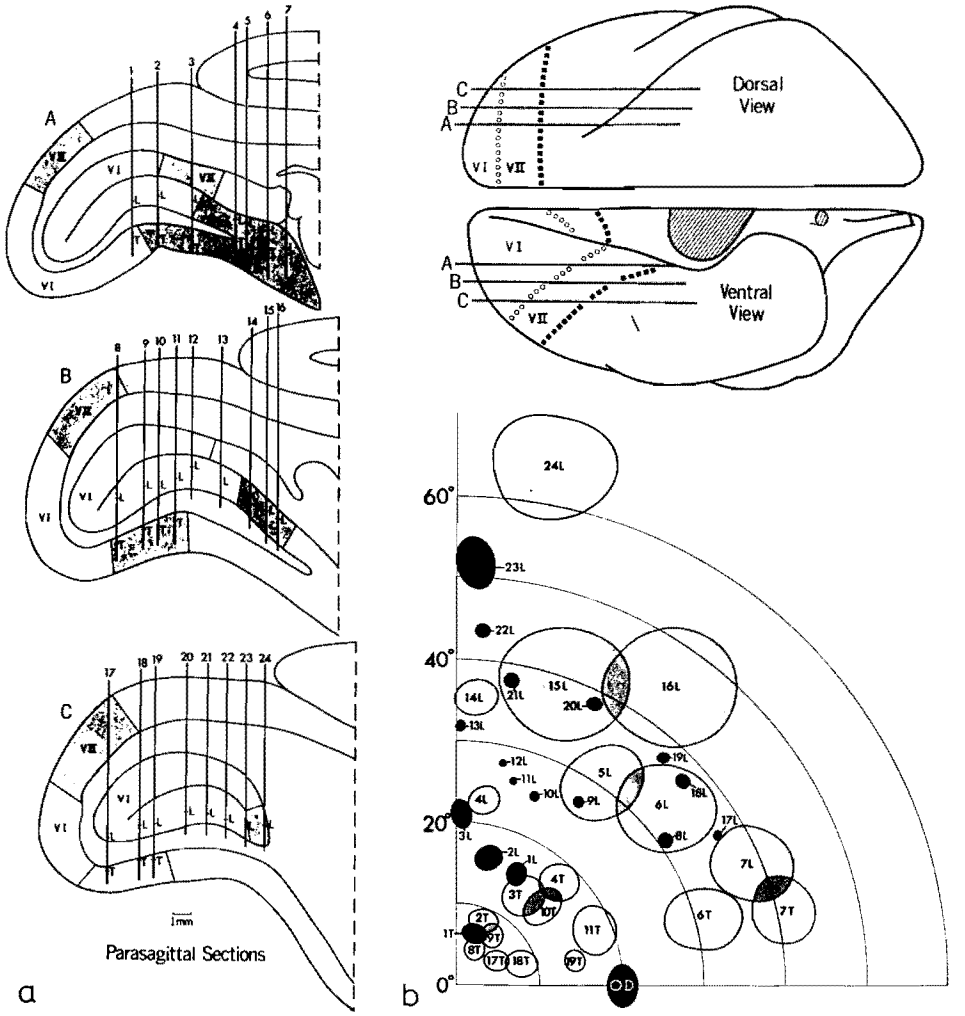

Fig. 3. Receptive fields for recording sites in V I and V II on the lower bank of the calcarine sulcus and tentorial surface on the left occipital lobe. a: diagrams A, B and C are drawings of parasagittal sections through the left occipital lobe. Drawing A was made from owl monkey 72-201; drawings B and C were made from owl monkey 72-343. Anterior is to the right in these sections. Microelectrode penetrations are indicated by numbered vertical lines and recording sites are marked by horizontal bars across these lines. 'L' indicates a recording site in the lower bank of the calcarine sulcus; 'T' indicates a recording site in the tentorial surface of the occipital lobe. b: receptive fields corresponding to the recording sites are shown in the perimeter chart in which the central 60° of the upper right visual quadrant is displayed. The locations of parasagittal sections A, B and C are shown in the dorsal and ventral views of the left cerebral hemisphere on the opposite page. In the ventral view, the brain stem and cerebellum have been removed to expose the ventral or tentorial surface of the occipital lobe.

parts of V II were explored were used to establish the limits and visuotopic organization of different parts of V II. Receptive field locations were used to determine the position of visual field coordinates as they relate to visual cortex, and these coordinates were transposed to surface views of parts of V II and then to an enlarged model of the

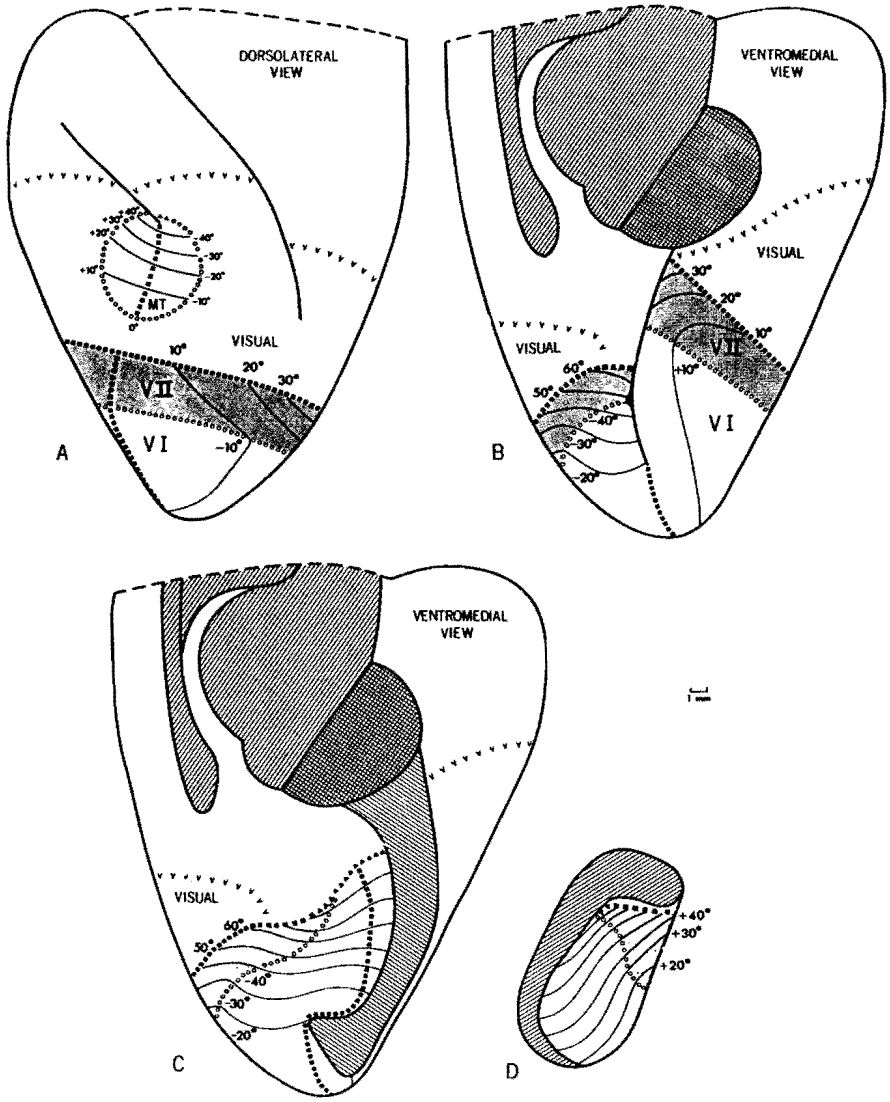

Fig. 4. Summary diagram illustrating the representations of the visual field in V I, V II and MT in the owl monkey. Diagram A is a dorsolateral view of the posterior two-thirds of the left cerebral hemisphere. Diagram B is a ventromedial view of the posterior two-thirds of the left cerebral hemisphere in which the brain stem and cerebellum have been removed to expose the ventral or tentorial surface of the occipital lobe. Diagram C is a similar ventromedial view in which the lower bank of the calcarine sulcus has been removed to expose visual cortex on the upper bank of the calcarine sulcus. Diagram D is a dorsal view of the lower bank of the calcarine sulcus, which has been removed from the brain. The small circles indicate the representation of the vertical meridian of the visual field; the black squares indicate the representation of the horizontal meridian of the contralateral hemifield; the black triangles indicate the representation of the temporal periphery of the contralateral hemifield. The rows of VVVVV indicate the anterior limits of visual cortex. Anterior is up in all of the diagrams.

posterior half of the brain. Fig. 4 shows the brain (or the model) in several stages of dissection, and thus, normally hidden parts of V II are shown in surface views.

The second visual area is shown in Fig. 4 as a distortion of visual field coordinates. Such a representation of the data obviously has limits, but it usefully illustrates several major conclusions. The central 7° of the horizontal meridian relate to a zone of cortex across the width of V II on the dorsolateral surface (Fig. 4A). The representation of the horizontal meridian then splits to form almost the entire anterior border of V II. The posterior border of V II is formed by the vertical meridian, and this border is coextensive with the portion of the border of V I that represents the vertical meridian. Thus, V II does not completely surround V I, and, as shown in Fig. 4C, a portion of the upper bank of the calcarine sulcus relates to the representation of the extreme temporal periphery of the visual field in V I, and this part of V I is not bordered by V II.

It is apparent from Fig. 4 that central parts of the lower visual quadrant are represented in dorsolateral V II and more peripheral parts of the lower quadrant are represented in the extension of V II on the medial wall and upper bank of the calcarine sulcus. The central parts of the upper visual quadrant are represented in the extension of V II on the ventral surface and the peripheral parts on the lower bank of the calcarine sulcus. It is also clear that proportionally more tissue in V II represents central rather than peripheral parts of the visual field.

Relation of V II to area 18

Previously we reported that a single histological type of cortex, area 18, borders area 17 (V I) along the representation of the vertical meridian in area 17 but *not* along the remaining margin of area 17 which corresponds to the representation of the extreme temporal periphery of the visual field. The electrophysiological mapping experiments indicate that V II is a narrow belt about 45 mm long and 3 mm wide except where it tapers at the ends. Area 18 is coextensive with the electrophysiologically defined V II and can be identified by the rather densely packed cells in layers IV and VI, which stand out in contrast to the less densely packed layer V (see Fig. 5). In sections stained for myelinated fibers, both the outer and inner bands of Baillarger are well developed (Fig. 5).

Area 18 is easy to distinguish from area 17 or striate cortex (see Fig. 5 and also ref. 1, Fig. 7 and ref. 2, Figs. 7 and 9). Area 18 is also quite different in structure from the small zone of cortex that borders both area 17 and area 18 in the calcarine sulcus (see ref. 2, Figs. 7 and 9). Since the IVth layer of cells and the bands of myelinated fibers are poorly developed in this small zone of cortex, it more closely resembles limbic cortex than area 18 (see ref. 2). This small zone of 'limbic' cortex, which lies immediately anterior to areas 17 and 18 in the calcarine sulcus, appears to correspond to the area 'prostriata' of Vitzthum and Sanides[29].

The description of architectonic differences between area 18 and the visual cortex immediately anterior to area 18 on the dorsal, medial and tentorial surfaces of the occipital lobe is complicated by the fact that a minimum of 5 distinct cortical visual areas adjoin the anterior border of area 18 in the owl monkey. Each of these visual

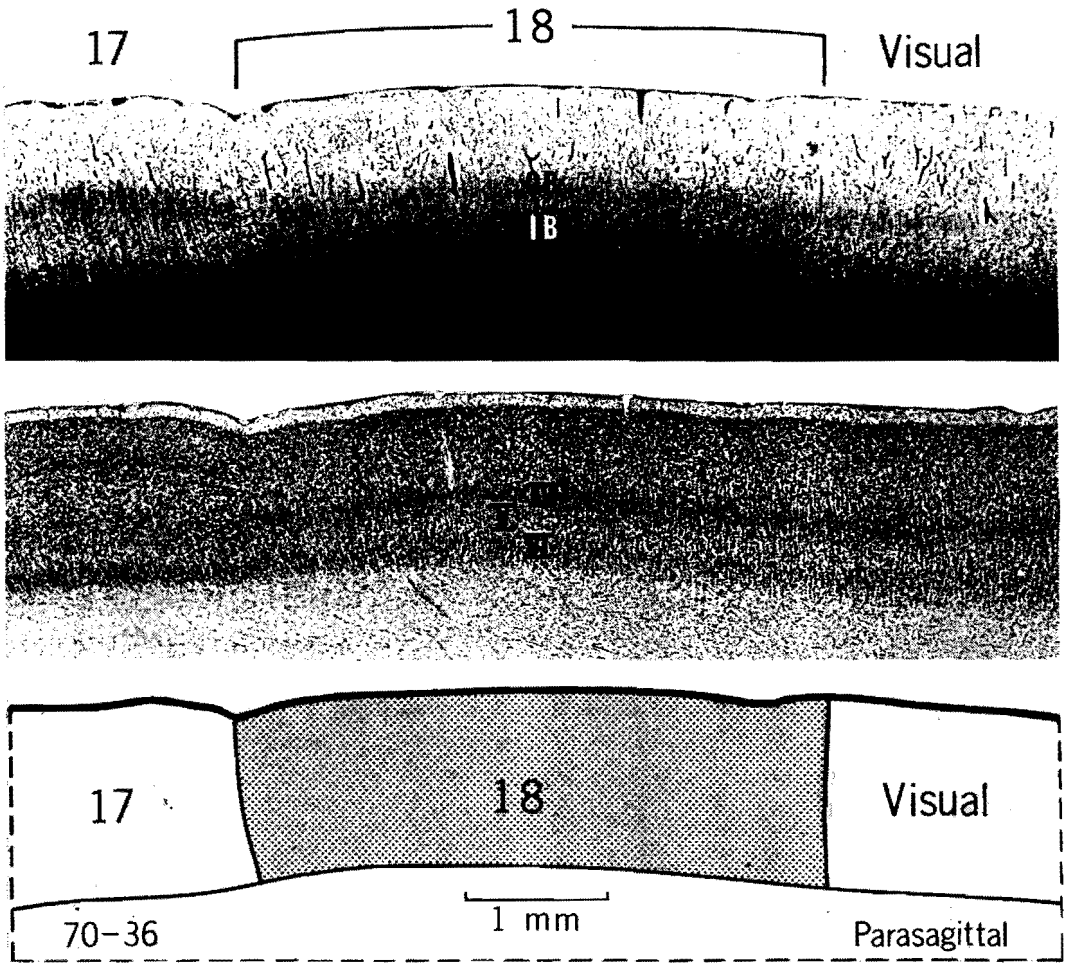

Fig. 5. Photomicrographs of adjacent parasagittal sections corresponding to row 3 of recording sites in owl monkey 70-36 which is illustrated in Fig. 1. The upper section was stained with hematoxylin for myelin; the lower section was stained with thionin for cell bodies. Anterior is to the right in these sections. Roman numerals IV, V and VI denote cortical layers. 'OB' indicates outer band of Baillarger; 'IB' indicates inner band of Baillarger.

areas contains its own separate representation of the visual field and its own distinct architectonic structure[4,6]; together these areas, which adjoin the anterior border of V II, comprise what we term the 'third tier' of cortical visual areas*. One of these 'third tier' areas, the dorsolateral crescent (DL), relates to MT, which is a first order transformation, just as V II relates to V I. DL is an elongated belt; its vertical meridian representation adjoins that of MT and its horizontal meridian representation is split. Thus, DL is another second order transformation of the contralateral hemifield[4]. Detailed descriptions of the distinctions between area 18 and each of the 'third tier'

* Primary visual cortex (V I) constitutes the first tier; V II constitutes the second tier.

visual areas will be taken up in forthcoming papers on these areas. An example of such a distinction is shown in Fig. 5 in which the sections illustrated correspond approximately to the cortical tissue recorded from row 3 of Fig. 1. In the visual cortex anterior to area 18 (V II), the outer band of Baillarger is not as well developed and the cells are slightly less packed in layers IV and VI. However this set of distinctions between V II and the visual cortex on its anterior border is valid for only this central region on the dorsal surface.

DISCUSSION

The organization of V II in primates

The electrophysiological results indicate that V II forms a long narrow belt surrounding most of V I. The representation of the horizontal meridian extends across the middle of this belt from the representation of the center of gaze at the dorsolateral border of V I so as to divide V II into a dorsal portion including the upper bank of the calcarine sulcus which systematically represents the lower visual quadrant, and a ventral portion including the tentorial surface and the lower bank of the calcarine sulcus which represents the upper visual quadrant. The representation of the horizontal meridian then splits to form the outer or anterior boundary of V II (see Figs. 4 and 6).

Few previous electrophysiological data are available to support the present evidence on the nature of the representation of the visual field in V II in primates (see p. 249), but anatomical studies[11,23,24,28,33] employing silver degeneration stains demonstrate that striate cortex projects in a systematic fashion onto V II and that the portion of striate cortex corresponding to the representation of the horizontal meridian projects to the anterior or outer border of V II. In addition, Cowey[10] has electrically stimulated various points in striate cortex of the squirrel monkey and mapped the regions in prestriate cortex which were activated by this focal stimulation, and the data illustrated in Fig. 8 of Cowey's report are consistent with the pattern of projections observed in the anatomical studies of the projection of V I onto V II in primates[11,23,24,28,33]. Our own unpublished electrophysiological mapping studies of V II in rhesus monkeys and galagos also indicate that at least part of the anterior border of V II in these primates represents the horizontal meridian as in owl monkeys. Thus, it seems reasonable to conclude that the pattern of organization seen in V II of owl monkeys exists in other primates even though this organization has not yet been determined in detail in other primates.

First and second order transformations of the visual field

The electrophysiological results from owl monkeys, supported by information concerning V II in other primates, indicate that the visuotopic organization of V II is fundamentally different from V I. In order to delineate precisely this difference, it is useful to consider a basic concept of topology. In their book, *Geometry and the Imagination*, Hilbert and Cohn-Vossen[14] state: 'Let us imagine a figure that can be distorted as much as we please but cannot be torn or cemented.' If a figure can be

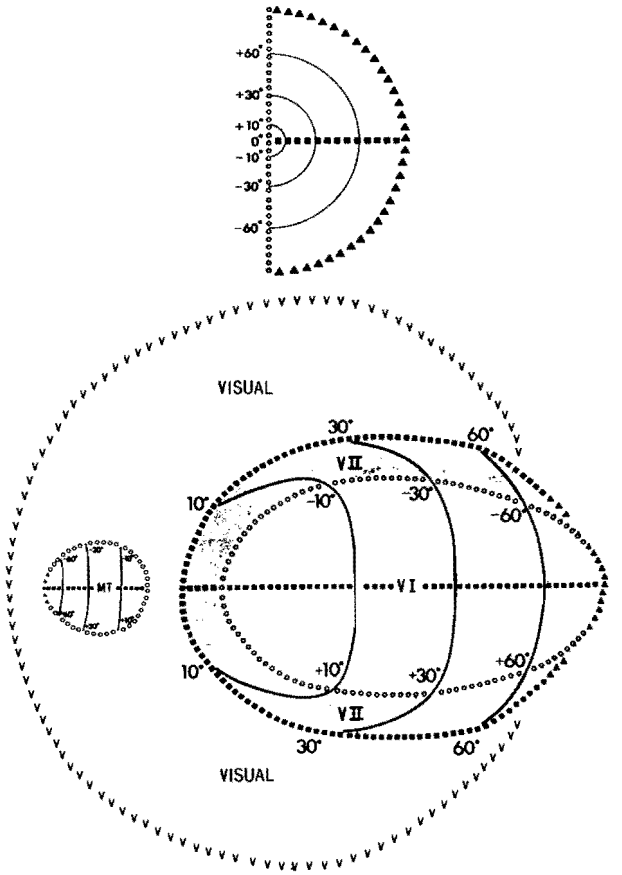

Fig. 6. The representations of the visual field in V I, V II and MT in the unfolded visual cortex of the owl monkey. The upper diagram is a perimeter chart of the contralateral half of the visual field. Below is a conceptual scheme for the unfolded visual cortex of the owl monkey. The unfolded visual cortex is approximately a hemispherical surface, which is viewed from above in this diagram. All conventions and abbreviations are the same as in previous figures.

transformed into another without being 'torn or cemented', the two figures are said to be topologically equivalent; if not, they are topologically non-equivalent. This is precisely the difference between the transformations of the contralateral hemifield into V I and into V II. V I is *topologically equivalent* to the contralateral half of the visual field and we refer to this as a *first order transformation* of the visual hemifield. V II is *topologically non-equivalent* to the contralateral half of the visual field and is termed a *second order transformation* of the visual hemifield. The basic difference between V I, a first order transformation of the visual hemifield, and V II, a second order transformation, is shown in Fig. 6 where the visual cortex is schematically unfolded. It is apparent that the primary visual area, V I, represents the contralateral half of the visual field in a topologically equivalent manner. That is, any row of points in the contralateral hemifield would correspond to a similar row of points in V I. However, the relative distances between the points in the visual field and points in

V I would not always correspond, since V I is a distorted representation of the visual hemifield. In Fig. 6, V I is shown as a distortion of the standard visual field perimeter chart in order to illustrate the large proportion of V I devoted to the central 10° of the visual hemifield and the smaller amounts devoted to more peripheral portions of the visual field. The smaller middle temporal visual area (MT) is organized like a miniature V I[1,3] and is also a first order transformation of the visual hemifield. V II, like V I, has an expanded representation of the more central parts of the visual field, but unlike V I, the representation of the horizontal meridian, except for the central 7°, is split and forms most of the outer border of V II. This split representation of the horizontal meridian in V II violates the principle of topological equivalence. Any row of points in the contralateral hemifield which crosses the horizontal meridian more than 7° from the center of gaze is broken into *two* rows of points in V II.

The functional significance of V II as a second order transformation

It is obvious that the shape of V II as a long narrow belt constrains the nature of possible representations of the visual hemifield (see Fig. 6) and poses a natural question about the significance of that shape. The greatly elongated form of V II in primates is the result of a relation of V II and V I that appears to have been maintained throughout the course of mammalian evolution in many separate lines of descent. In so far as is known, V II borders V I along the portion of V I that represents the zero vertical meridian (*i.e.*, the line of decussation of the retina) in all mammals (see ref. 2 for review). In those species of mammals with major expansion of the amount of cortex devoted to frontal vision, most of the border of V I is related to the vertical meridian. In the owl monkey, for example, 90% of the border of V I represents the vertical meridian[2], while only 10% is devoted to the extreme temporal periphery. Even here, V II retains its common border with V I along the representation of the vertical meridian although this results in a considerable elongation of V II. The maintained relation of V II to V I in spite of the distortion of the form of V II suggests that the common border along the representation of the vertical meridian may be of great functional importance.

In the lateral geniculate nucleus[18], inferior pulvinar[5], superior colliculus[21], V I[2] and MT[1,3], the visuotopic map is topologically equivalent to the contralateral visual hemifield, and thus adjacent parts of the visual hemifield are always represented in adjacent parts within these structures. This topologically equivalent visuotopic organization would permit neurons representing adjacent parts of the visual field to interact over short axonal and dendritic pathways. However V II is not topologically equivalent to the contralateral hemifield, and adjacent parts of the visual hemifield are *not* always represented in adjacent parts of V II. This finding, together with the existence of the long common border of V I and V II coextensive with the representation of the vertical meridian and the resulting elongated form of V II, suggests that it is more important for parts of V II representing any given portion of the contralateral hemifield to be located in close proximity to the parts of *V I* representing the *same* portions of the hemifield than it is for parts of V II to be located near other parts of V II representing adjacent portions of the visual field. Viewed in this perspective, V II

appears to be an adjunct of V I in that it is the relationship of V II to V I which seems to be the overriding consideration governing the visuotopic organization of V II. Thus, it can be seen in Fig. 7 that the type of representation found in V II allows homotopic parts of V I and V II to be interconnected over relatively short pathways. In a similar manner, we have noted that the formation of 'leaflets' or 'subsidiary laminae' in the dorsal lateral geniculate nucleus of some primates argues for the importance of short neural pathways interconnecting neurons representing the same parts of the visual field via opposite eyes[18]. While it would be theoretically possible to maintain both the common border of V I and V II along the vertical meridian and a topologically equivalent representation in V II, both long interconnections and rather extreme distortions of the representation of the temporal periphery of the visual field would result (see Fig. 7). If V II did not border V I all along the representation of the vertical meridian, distortions could be reduced, but longer interconnections would be required.

It is known from both fiber degeneration studies by Tigges *et al.*[27] that homotopic areas of V I and V II in New World monkeys are reciprocally connected and that cells of the supragranular layers of cortex form most of the interconnections[24,27]. It is of further interest that projections from area 17 were found to terminate in layer IV and the deeper parts of layer III of area 18 while projections from area 18 terminate within layer I of area 17 (ref. 27) where they presumably contact the apical dendrites of pyramidal cells. Thus, we have a system where relatively unprocessed information in V I could be relayed over short pathways to homotopic locations in V II for further computations and the results could then be relayed back to V I to modulate the activity of pyramidal cells as they transmit information to other cortical and subcortical centers. In this view, V II is seen functionally as performing an important role in modifying the outflowing activity of V I. However, the second visual area also projects to cortical areas other than V I in New World monkeys (J. Tigges, personal communication), and we do not suggest that the only function of V II is to modify the activity of neurons in V I.

Finally, it is important to point out that the principle of topological representation of the visual space is not completely lost in V II. The representations of the upper and lower quadrants of the visual hemifield *are separated* from each other in V II so that neurons in V II representing space just above or just below the horizontal meridian cannot interact over short axon or dendritic pathways. However, each arm of the V II belt topologically represents a visual quadrant and the central 7° or so of the visual hemifield is topologically represented in V II. Therefore, interactions over short distances are possible for neurons representing space within the upper or lower quadrant in V II, and it is significant, as is apparent in the summary diagram of Fig. 6, that neurons representing the central 7° of visual field just above or just below the horizontal meridian in V II can also interact.

The visuotopic organization of V II in other mammals

In the early investigations of V II in cats and rabbits, it was concluded that the visuotopic organization of V II was a relatively simple mirror image of V I[25,26]. The

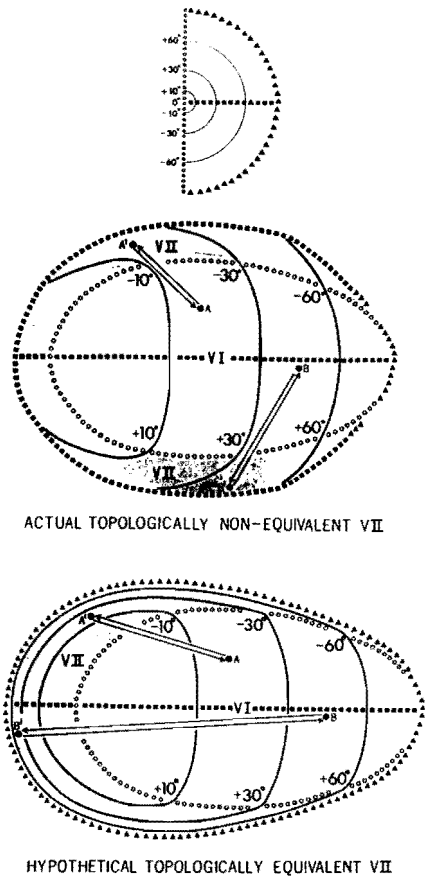

Fig. 7. The actual topologically non-equivalent V II and a hypothetical topologically equivalent V II. The same relative amounts of cortical tissue are devoted to the various parts of the visual field in the hypothetical V II as in the actual V II, and the temporal periphery of the contralateral half of the visual field is represented in the extremely thin outer margin of this hypothetical V II. A and A′ and B and B′ are homotopic loci in V I and V II. The arrows indicate reciprocal connections between these homotopic loci. All other conventions are the same as in previous figures.

first findings indicating that V II might not be a simple mirror image of V I were reported by Hubel and Wiesel[15] for the cat in 1965. These authors made a number of medio-lateral rows of closely spaced microelectrode penetrations across the visual cortex of the cat. Near the border between V I and V II, the receptive fields were located near the vertical meridian of the visual field as expected, but moving laterally across V II, the receptive fields proceeded to only 15° from the vertical meridian in some rows. In still more laterally placed penetrations, the progressions of receptive fields tended to move back toward the vertical meridian. Hubel and Wiesel considered the site of reversal in the progression of receptive fields as the border between V II and another area, V III, located lateral to V II. However, the border between V II and V III clearly did not correspond to the extreme temporal periphery of the visual field since the reversals in receptive field progressions were sometimes only 15° from the vertical

meridian. In 1967, Bilge and his collaborators[7] reported that most of the border between V II and V III in the cat corresponds to a representation of the horizontal meridian. Unfortunately these authors did not publish receptive field data to support their summary diagram. However, their conclusion is supported by Garey, Jones and Powell's[12] finding in the cat that the lateral part of area 18 projects to the representation of the horizontal meridian in the superior colliculus. On the other hand, evoked potential mapping studies[30] and some of Hubel and Wiesel's electrophysiological data[15] do not appear to completely support the view that the lateral border of V II in the cat corresponds to the horizontal meridian since receptive fields for neurons at the lateral border of area 18 did not always adjoin the horizontal meridian. Furthermore, only a limited part of V II has been explored with recording electrodes. Thus, some aspects of the representation in the second visual area of the cat remain in doubt.

The findings of Hall *et al.*[12] for the visual cortex of the grey squirrel are similar to Hubel and Wiesel's[15] for the cat in that receptive fields recorded near the lateral edge of V II in the squirrel were sometimes only 15° from the vertical meridian. As in the cat, a third visual area with a reversed visuotopic organization adjoins at least part of V II on its lateral border, but in the squirrel much of the lateral border of V II clearly does not correspond to a representation of either the extreme temporal periphery or the horizontal meridian of the visual field. Although more temporal parts of the visual field are represented toward the anterior and posterior ends of V II, one is led to suspect that in the squirrel, and possibly in the cat, some of the more temporal parts of the visual field, especially near the horizontal meridian, simply are not represented in V II. Recordings from V II of the tree shrew[20] suggest that it is organized very much like V II of the squirrel, and recordings from V II of the hedgehog also show that the area is not a simple mirror image of V I[19]. On the other hand, in early surface recordings from V II of the rabbit it appeared that V II might be a simple mirror image of V I in these mammals[26]. However, even in the rabbit, recent microelectrode mapping studies now indicate that only 30° of visual field are represented across the width of the mid-portion of V II and that much of the lower and upper quadrants of the visual hemifield are separated at opposite ends of the V II belt[32]. Thus, in those mammals for which some detail is known of the organization of V II, it appears that the area is not a simple topological transformation of the visual hemifield as is V I.

ACKNOWLEDGEMENTS

We thank Dr. Leon Schmidt, Southern Research Institute, Birmingham, Alabama for providing the owl monkeys used in this study. Histological materials were prepared by Mrs. I. Lucey and Mrs. J. Ekleberry. Figures were drawn by Ms. D. Urban and photographic work was by Mr. T. Stewart. We thank Dr. R. W. Guillery for providing helpful comments on the manuscript and Dr. R. H. Lane for assisting during some of the experiments.

This study was supported by NINDS Grants NS-05326 and NS-06225, NICHD Grant HD-03352, and NSF Grant GB-36779.

NOTE ADDED IN PROOF

After submitting this paper, a report on area 18 of the cat appeared[28A]. According to Tusa, the lateral border of area 18 in the cat does not correspond to the horizontal meridian and the most temporal part of the visual hemifield does not appear to be represented in area 18.

Also, we have briefly described another third tier visual area forming part of the anterior border of V II of the owl monkey[2A].

REFERENCES

1 ALLMAN, J. M., AND KAAS, J. H., A representation of the visual field in caudal third of the middle temporal gyrus of the owl monkey *(Aotus trivirgatus)*, *Brain Research*, 31 (1971) 85–105.

2 ALLMAN, J. M., AND KAAS, J. H., Representation of the visual field in striate and adjoining cortex of the owl monkey *(Aotus trivirgatus)*, *Brain Research*, 35 (1971) 89–106.

2A ALLMAN, J. M., AND KAAS, J. H., A visual area adjoining the second visual area, V II, on the medial wall of parieto-occipital cortex of the owl monkey, *Aotus trivirgatus*, *Anat. Rec.*, 178 (1974) 297–298.

3 ALLMAN, J. M., KAAS, J. H., AND LANE, R. H., The middle temporal visual area (MT) in the bushbaby *(Galago senegalensis)*, *Brain Research*, 57 (1973) 197–202.

4 ALLMAN, J. M., KAAS, J. H., LANE, R. H., AND MIEZIN, F. M., A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey *(Aotus trivirgatus)*, *Anat. Rec.*, 175 (1973) 263–264.

5 ALLMAN, J. M., KAAS, J. H., LANE, R. H., AND MIEZIN, F. M., A representation of the visual field in the inferior nucleus of the pulvinar in the owl monkey *(Aotus trivirgatus)*, *Brain Research*, 40 (1972) 291–302.

6 ALLMAN, J. M., KAAS, J. H., AND MIEZIN, F. M., A dorsomedial visual area adjoining V[illegible] owl monkey *(Aotus trivirgatus)*, *Soc. Neurosci. Abstr.*, 1 (1971) 126.

7 BILGE, M., BINGLE, A., SENVIRATNE, K. N., AND WHITTERIDGE, D., A map of the visual cortex in the cat, *J. Physiol. (Lond.)*, 191 (1967) 116P–117P.

8 BRODMANN, K., *Vergleichende Lokalisationslehre der Grosshirnrinde*, Barth, Leipzig, 1909, 324 pp.

9 CAMPBELL, A. W., *Histological Studies on the Localization of Cerebral Function*, Cambridge University Press, Cambridge, Mass., 1905, 360 pp.

10 COWEY, A., Projection of the retina on to striate and prestriate cortex in the squirrel monkey *(Saimiri sciureus)*, *J. Neurophysiol.*, 27 (1964) 366–396.

11 CRAGG, B. G., AND AINSWORTH, A., The topography of the afferent projections in circumstriate visual cortex of the monkey studied by the Nauta method, *Vision Res.*, 9 (1969) 733–747.

12 GAREY, L. J., JONES, E. G., AND POWELL, T. P. S., Interrelationships of striate and extrastriate cortex with the primary relay sites of the visual pathway, *J. Neurol. Neurosurg. Psychiat.*, 31 (1968) 135–157.

13 HALL, W. C., KAAS, J. H., KILLACKEY, H., AND DIAMOND, I. T., Cortical visual areas in the grey squirrel *(Sciurus carolinesis)*: a correlation between cortical evoked potential maps and architectonic subdivisions, *J. Neurophysiol.*, 34 (1971) 437–452.

14 HILBERT, D., AND COHN-VOSSEN, S., *Geometry and the Imagination*, Chelsea, New York, 1952, 357 pp.

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

16 HUBEL, D. H., AND WIESEL, T. N., Stereoscopic vision in macaque monkey, *Nature (Lond.)*, 225 (1970) 41–42.

17 HUGHES, A., Topographical relationships between the anatomy and physiology of the rabbit visual system, *Docum. ophthal. (Den Haag)*, 30 (1971) 33–160.

18 KAAS, J. H., GUILLERY, W. R., AND ALLMAN, J. M., The representation of the optic disc in the dorsal lateral geniculate nucleus: a comparative study, *J. comp. Neurol.*, 147 (1973) 163–180.

19 KAAS, J. H., HALL, W. C., AND DIAMOND, I. T., Cortical visual areas I and II in the hedgehog: