REPRESENTATION OF THE VISUAL FIELD IN STRIATE AND ADJOINING CORTEX OF THE OWL MONKEY *(AOTUS TRIVIRGATUS)*

JOHN M. ALLMAN AND JON H. KAAS

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

(Accepted June 18th, 1971)

INTRODUCTION

Topographical representation of the visual field within striate cortex of primates has been demonstrated by a number of methods. In man, visual field deficits have been related to cortical lesions[10,27] and the perceived positions of evoked sensations have been related to sites of electrical stimulation[2]. In monkeys anterograde or retrograde degeneration techniques have been used to determine separately retinogeniculate[3] and geniculostriate relations[20,21]. While clinical and anatomical procedures are useful in revealing the general organization of striate cortex, electrophysiological mapping methods permit a full and detailed exploration of a cortical representation. Early electrophysiological experiments with surface electrodes were restricted to cortex accessible on the dorsolateral surface of the brain[26]. In later investigations with penetrating electrodes, results were reported for only a few recording sites in the buried cortex of the calcarine sulcus[4,7,12]. Thus, the primary goal of the present investigation was to explore completely the striate cortex in a primate using electrophysiological mapping techniques. An additional purpose was to compare the visuotopic organization of striate cortex of the owl monkey, as the only nocturnal monkey[18], with the organization reported for other monkeys.

Another goal of the present experiments concerns the representation of the visual field in the cortex that borders striate cortex. A second representation of the visual field, visual area II (V II), has been described in cortex adjacent to striate cortex in a number of mammals[1,4,8,11,14,15,24,25,28,34,36], and this second area has been identified with a distinct architectonic zone, area 18[4,8,11,14,15,24,25,28,34]. While area 18 has been traditionally described as completely surrounding striate cortex in primates (for review, see Zeki[35], and Sanides[22]), recent studies indicate that a small portion of striate cortex of the calcarine sulcus is not bordered by area 18[22,29]. As early as 1947, it was predicted area 18 or V II would not completely surround striate cortex or V I in primates (see ref. 33, p. 533). Furthermore, this prediction is consistent with the results of electrophysiological studies in the rabbit[28], hedgehog[14], squirrel[8], tree shrew[15], and cat[34] where V II was found to border only the portion of the margin of striate cortex that represents the zero vertical meridian (*i.e.*, the line of decussation of the retina). However, there is little direct information on the relation of V II to V I in primates. Using electrophysiological mapping methods, Cowey[4] was able to demonstrate a second visual area adjoining striate cortex on the dorsal surface of the occipital lobe of the squirrel monkey but was not able to demonstrate this prestriate area adjacent to striate cortex on the medial surface of the brain. Other reports on the visuotopic organization of prestriate cortex in primates have also been limited to the region bordering striate cortex of the dorsal surface[1,5,13,16,24,34,35]. In the present study, an attempt was made to determine the full extent of striate cortex bordered by V II.

METHODS

The procedures have been described previously[1]. Representations of the visual field in striate cortex and in the adjoining sectors of area 18 were determined with electrophysiological mapping methods in 28 owl monkeys, anesthetized with urethane. In many of these experiments, additional cortical areas were explored and these results will be reported elsewhere. Microelectrodes were used to record from small clusters of neurons or occasionally from single neurons, and receptive fields were determined by moving slits of light or bars of shadow on a translucent plastic hemisphere which defined the visual field of one eye. The other eye was sutured shut and covered with

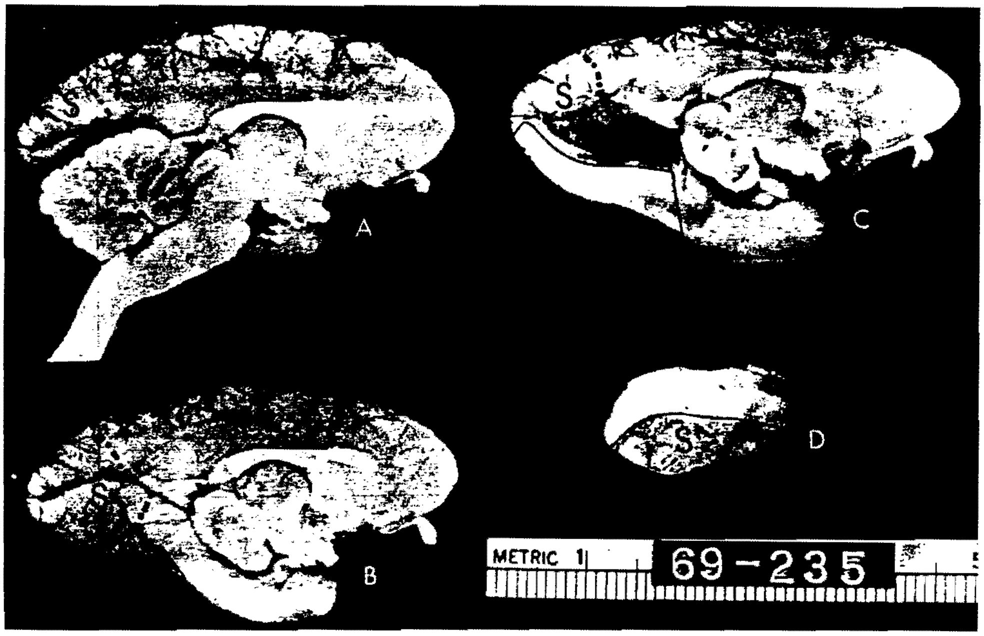


Fig. 1. Dissection of the owl monkey brain showing the location of striate cortex on the medial surface and in the calcarine sulcus of the cerebral hemisphere. Photograph A is a medial view of the owl monkey brain cut in half sagittally. In B the cerebellum and brain stem have been cut away to expose the tentorial surface of the occipital lobe. In C the lower bank of the calcarine sulcus has been removed to reveal the upper bank of the calcarine sulcus. In D the lower bank of the calcarine sulcus is shown. The rostral border of the striate cortex (S) is indicated by the dot–dash lines. The thin lines in C and D indicate where the brain has been cut to separate the lower bank of the calcarine sulcus from the upper bank.

an opaque shield. Most recordings were from cortex contralateral to the stimulated eye.

RESULTS

Striate cortex (area 17)

Location. The location and extent of striate cortex were determined from serial brain sections which were then used to construct an enlarged model of the brain. The border of striate cortex was indicated on the model and then transferred to photographs of another brain in several stages of dissection (Fig. 1). Striate cortex occupies the dorsal surface of the caudal occipital lobe, extends rostrally across the medial wall and tentorial surface, and continues rostrally as it extends laterally in calcarine sulcus, which is a simple fold in the medial surface of the cerebral hemisphere.

The visuotopic organization of striate cortex

The representation of the visual field in striate cortex was determined from 616 receptive fields mapped for clusters of neurons or single neurons in 343 electrode penetrations in 28 owl monkeys. A portion of the data is illustrated here to support the summary diagram of Fig. 5.

The organization of striate cortex of the dorsal surface of the occipital lobe is

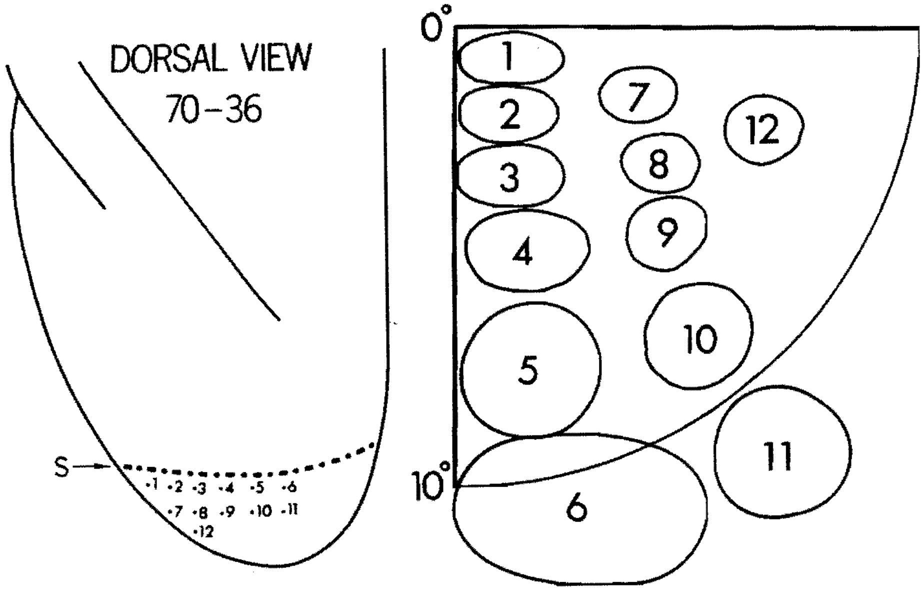


Fig. 2. Receptive fields for recording sites from the dorsal surface of the striate cortex of owl monkey 70–36. Right, numbered dots indicate the sites of microelectrode penetrations on a dorsal view of the caudal half of the right cerebral hemisphere on which medial is left, rostral is up and S indicates the rostral border of striate cortex. Left, receptive fields that correspond to the numbered recording sites are on a perimeter chart of the central 10° of the inferior temporal quadrant of the visual field of the right eye. Compare with Fig. 5.

indicated by the results of one experiment shown in Fig. 2. The center of gaze is represented on the extreme dorsolateral surface of occipital lobe near the border of

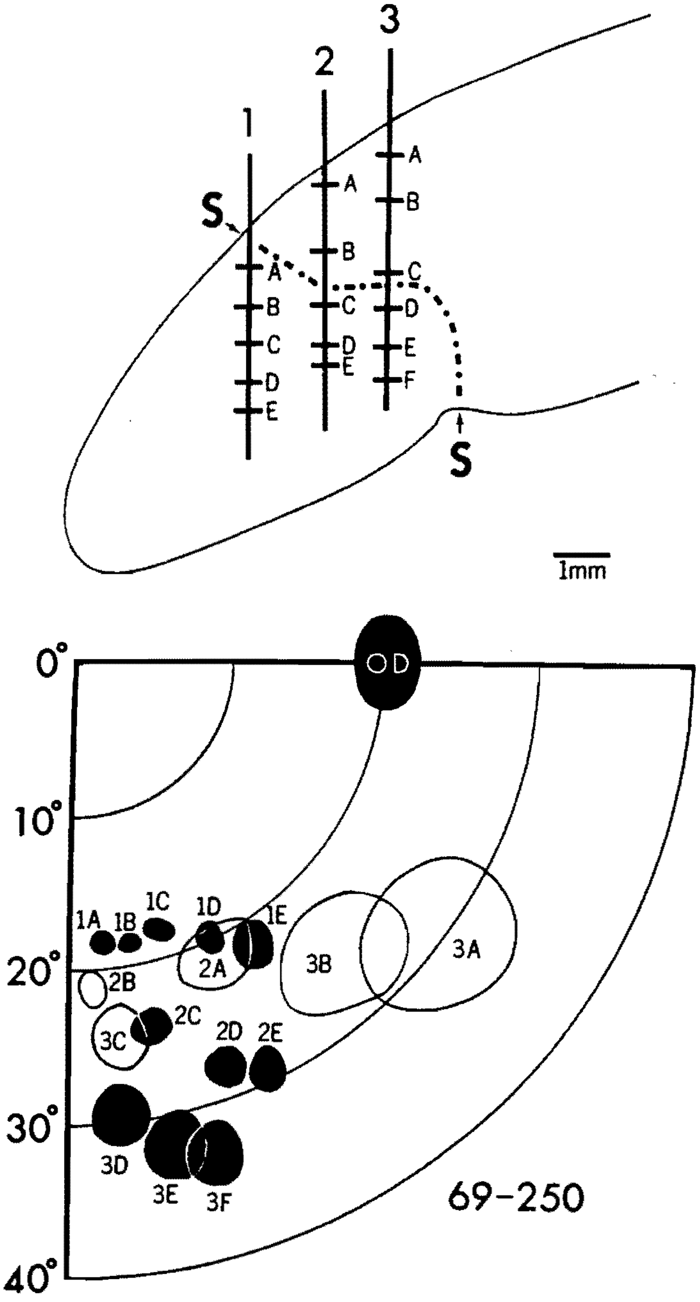


Fig. 3. Receptive fields for recording sites from striate cortex of the medial wall of the occipital lobe of owl monkey 69–250. Above, a parasagittal section through the cortex of the medial wall of the left occipital lobe approximately 1 mm lateral to the medial edge of the cerebral hemisphere. S marks the rostral margin of striate cortex. Occipital cortex below the calcarine sulcus does not extend medially to the plane of the section. Below, a perimeter chart of the central 40° of the inferior temporal quadrant of the visual field of the right eye. Receptive fields for recording sites in striate cortex are solid black; receptive fields mapped from area 18 (V II) are outlined. The solid black oval marked 'OD' indicates the projection of the optic disc in the visual field.

striate cortex (see receptive field 1, Fig. 2). Proceeding medially across the dorsal surface along the striate border, the representation of the visual field progresses inferiorly along the vertical meridian (receptive fields 1–6). Proceeding posteriorly across the dorsal surface, the representation progresses temporally in the contralateral half of the visual field and toward the horizontal meridian (receptive field 3, 8, 12). These results and those from other experiments indicate that a portion of the lower quadrant of the visual field within 15° of gaze is represented in the striate cortex of the dorsal surface of the occipital lobe.

The organization of the striate cortex of the left medial wall dorsal to the calcarine sulcus is shown in Fig. 3. The results indicate that the striate representation of the lower quadrant of the visual field is continued from the dorsal surface onto the cortex of the medial wall. As the striate boundary is approached, the receptive fields border the vertical meridian (see receptive fields 1A, 2C and 3D). Recording sites successively farther from the striate border correspond to receptive fields successively more temporal in the contralateral half of the visual field.

The 5 receptive fields for recording sites in prestriate cortex will be discussed in the next section.

The organization of the calcarine and tentorial surfaces of striate cortex is illustrated in Fig. 4. The portion of the upper quadrant of the visual field within 15–20° of the center of gaze is represented on the tentorial surface of striate cortex. Most of the lower quadrant and the temporal periphery of the upper quadrant are represented on the upper bank of the calcarine sulcus. The remaining intermediate portion of the upper quadrant is represented in the lower bank of the calcarine fissure.

Judging from the position of receptive fields near the blind spot in the visual field of the contralateral eye, the representation of this area of the visual field lies at the caudal tip of the calcarine sulcus at approximately the site where the tentorial surface, medial surface and banks of the calcarine sulcus adjoin one another. Thus in Fig. 4, the receptive fields for recording sites on the upper and lower banks of the caudal curvature of the calcarine sulcus in penetration 25 are just temporal to the projection of the optic disc (OD) in the visual field. Presumably, a small portion of striate cortex at the tip of the fold of the calcarine sulcus corresponds to the representation of the projection of the optic disc in the visual field and receives input from only the ipsilateral eye.

The data collected from other experiments are consistent with the results illustrated in Figs. 2–4. The results for striate cortex are combined and summarized in Fig. 5. Diagram 5A is a perimeter chart which is a planar representation of the contralateral half of the visual field. Diagram 5B illustrates the distortion of the representation of the visual field that occurs in striate cortex which is shown as an unfolded surface. When unfolded, striate cortex approximates one half of an ellipsoid. This approximation was obtained by spreading liquid latex on the surface of the striate cortex of a model of the brain which was constructed from drawings of serial brain sections. The latex was allowed to dry and then removed and unfolded. Thus, the contralateral half of the visual field, which as a surface may be considered as a quarter of a sphere, is transformed into half of an ellipsoid in the representation of half of the visual field in contralateral striate cortex. The manner in which the representation folds around the occipital lobe and into the calcarine sulcus is shown in parts C–F of Fig. 5. The figure indicates the great proportion of striate cortex devoted to central and paracentral vision. Approximately half of the area represents the central 20° of the visual field. As a result of this distortion of the visual field representation, the portion of the

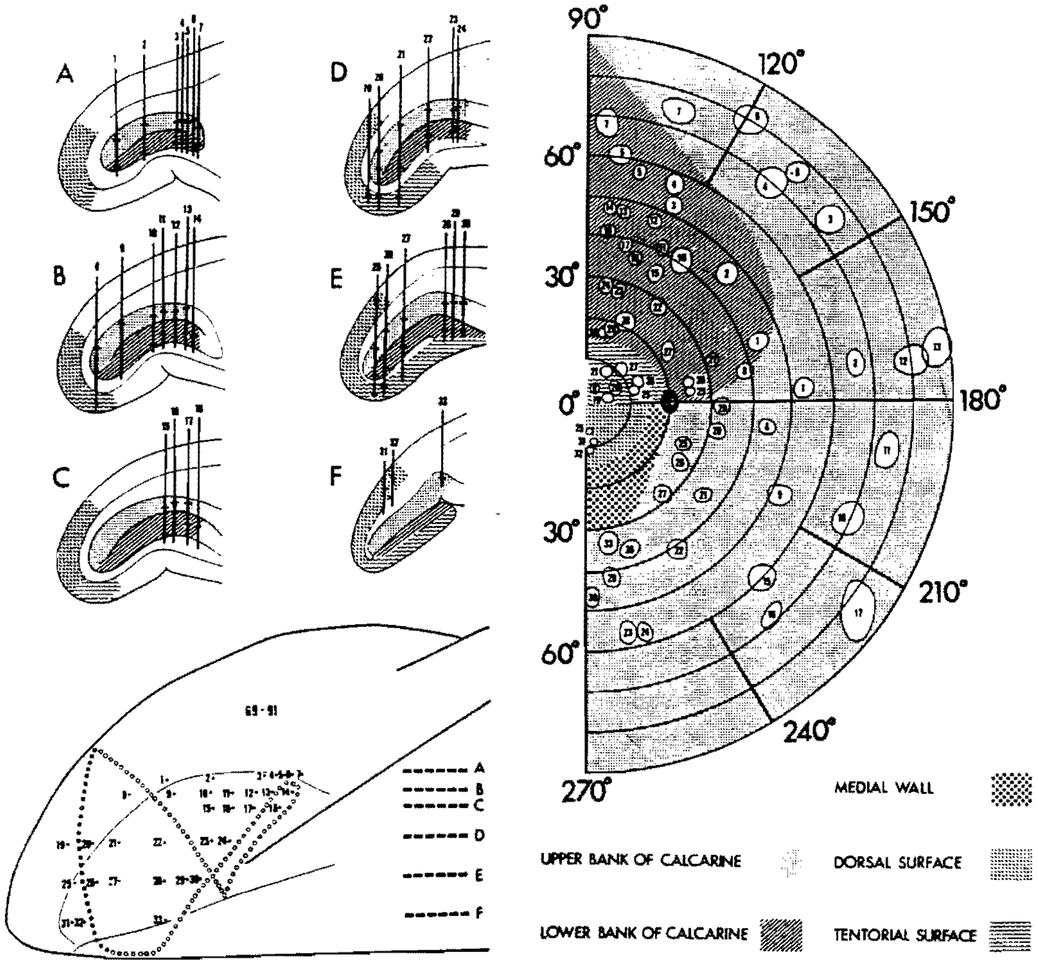


Fig. 4. Receptive fields for recording sites in striate cortex in owl monkey 69-91. Drawings A–F are of parasagittal brain sections containing microelectrode tracts 1–33. Electrode penetrations are indicated by numbered vertical lines and recording sites are marked by horizontal bars across these lines. Below these drawings, a dorsal view of the left occipital lobe shows the sites of the microelectrode penetrations and heavy dashed lines A–F indicate the levels from which the parasagittal sections above were taken. The thin lines in the dorsal view indicate the outline of the buried calcarine sulcus. The solid dot-dash line indicates the rostral border of the striate cortex which continues as a hollow dot-dash line on the tentorial surface, the lower and upper banks of the calcarine sulcus, and the medial wall of the occipital lobe. The receptive fields are plotted on a perimeter chart of the temporal half of the visual field of the right eye. The solid black oval marked 'OD' indicates the projection of the optic disc in the visual field. The different patterns (fine dots, waves etc.) mark subdivisions of striate cortex (A) which correspond to the subdivisions of the visual field as indicated on the perimeter chart. These relations were determined, in part, from other experiments (for example, the sector of visual field represented on the medial wall).

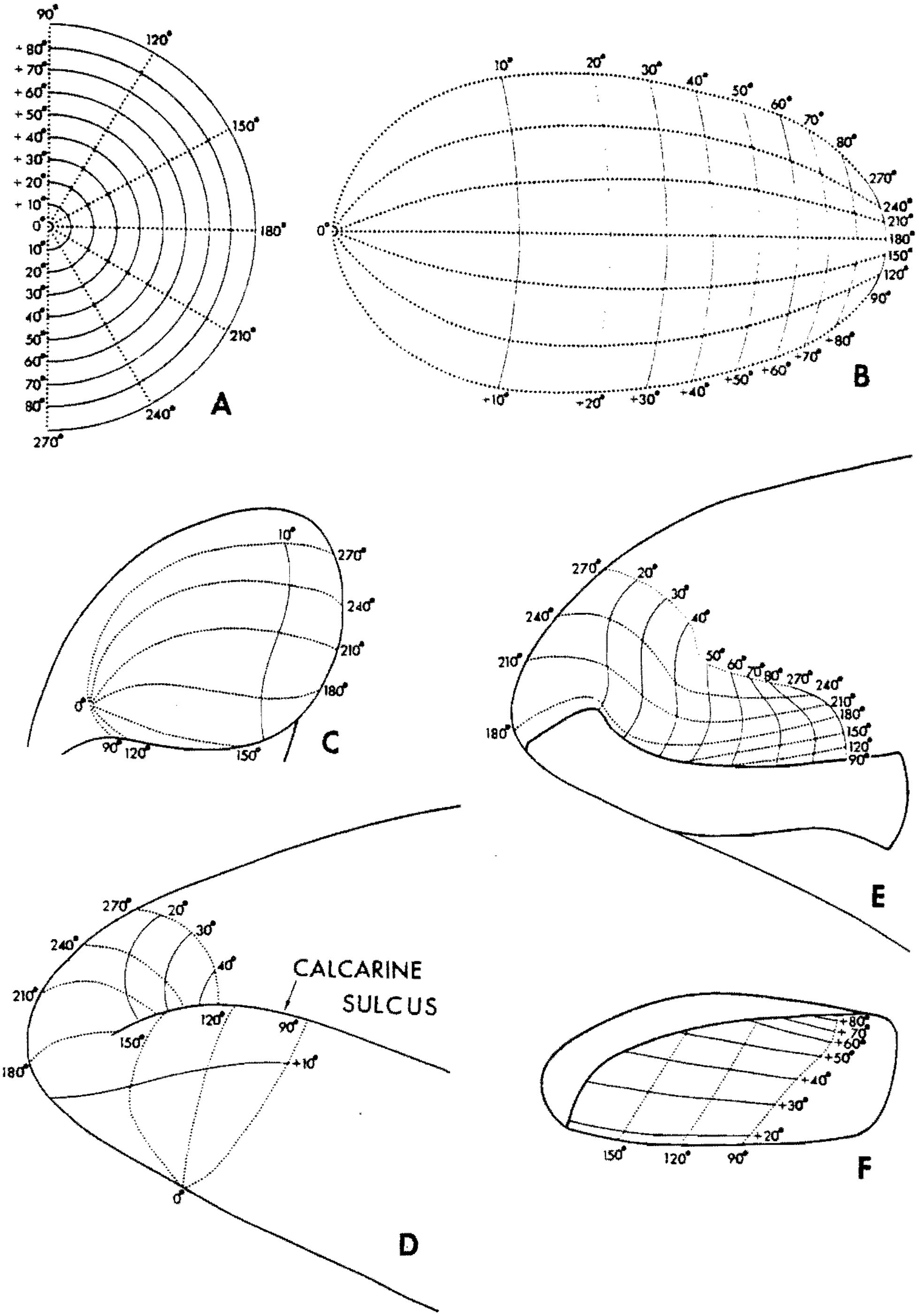
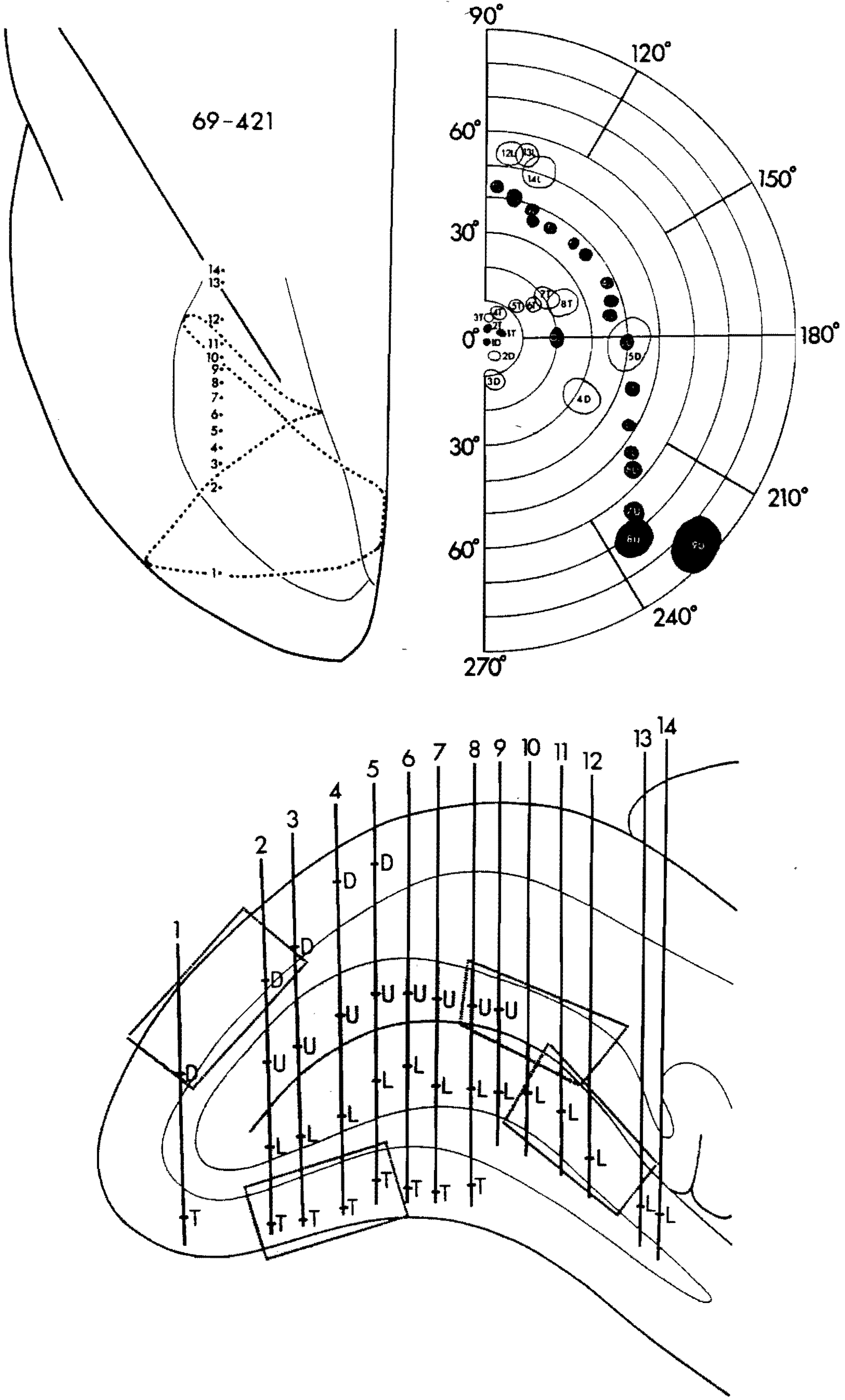


Fig. 5. Representation of the visual field in striate cortex of owl monkey. Diagram A is a planar representation of the contralateral half of the visual field, which may be thought of as a quarter of a sphere. Diagram B is a planar representation of unfolded striate cortex which is approximately one-half of an ellipsoid. The organization and location of striate cortex is shown in 4 views of the occipital lobe in stages of dissection below (C–F). Diagram C is a posterior view and D is a ventromedial view of the occipital lobe; in ventromedial view E, the lower bank of the calcarine fissure has been removed to expose the upper bank. The gray area indicates the brain cut made to remove the lower bank of the calcarine fissure. In F, the lower bank of the calcarine fissure, which has been removed from the brain, is viewed dorsally. Compare with Fig. 1.


69-421
1
2
3
4
5
6
7
8
9
10
11
12
13
14
90°
120°
150°
180°
210°
240°
270°
60°
30°
0°
30°
60°
D
U
L
T

striate border devoted to the vertical meridian is 9 times greater than the portion devoted to the temporal periphery. Yet the lengths of the corresponding regions in the retina or visual field are equal (*i.e.*, as meridians of a hemisphere).

An example of the reversal of visuotopic organization in cortex adjoining striate cortex can be seen in Fig. 3 where electrode penetrations 2 and 3 along the cortex of the medial wall of the occipital lobe pass from area 18 into area 17. In these electrode penetrations, recording sites farthest from the 17–18 border correspond to the receptive fields which are farthest from the vertical meridian. Thus, recording site A in penetration 3 was several millimeters rostral and dorsal to the striate border on the medial wall and the corresponding receptive field was almost 30° from the vertical meridian in the contralateral hemifield. Receptive fields for the two recording sites approaching the border of striate cortex, 3B and 3C, were successively closer to the vertical meridian. In area 17, receptive fields for recording sites D, E, and F proceed away from the vertical meridian. A similar reversal of visuotopic organization in cortex adjoining area 17 is indicated by the locations of the receptive fields for penetration 2 in Fig. 3. Other examples of reversals of visuotopic organization in cortex adjoining area 17 are illustrated in Figs. 6 and 8 (see also Figs. 7 and 8 of a previous report[1]).

Extent of the V I and V II border

As indicated on previous pages, 90% of the border of striate cortex of the owl monkey represents the zero vertical meridian and 10% represents the extreme temporal periphery of the contralateral half of the visual field. As is indicated in Figs. 3, 6 and 8, the second visual area, V II, adjoins V I along the portion of the border of V I that represents the vertical meridian. Thus, in Fig. 3, V II is shown to adjoin V I along the representation of the vertical meridian on the medial wall of the cerebral hemisphere. In Fig. 6, this is shown for the representation of the vertical meridian on the dorsal surface, tentorial surface, and lower bank of the calcarine sulcus. In Fig. 8, V II is shown to adjoin V I along the part of the upper bank of the calcarine sulcus that represents the vertical meridian. The results of other experiments are consistent with those illustrated and V II was found to border V I along both central and peripheral parts of the representation of the vertical meridian.

Fig. 6. Locations of visually responsive and nonresponsive juxtastriate cortex. Upper left, a dorsal view of the caudal two-thirds of the left cerebral hemisphere. Numbered dots mark vertical microelectrode penetrations. Thin lines indicate the location of the hidden calcarine sulcus and a broken line indicates the boundary of striate cortex as it extends from the dorsal surface along the tentorial surface, on the upper and lower banks of the calcarine sulcus and on the medial wall. Below, electrode tracts are marked by numbered vertical lines and recording sites by lettered horizontal bars on a parasagittal brain section cut in the plane of electrode penetrations 1–14. D, U, L, and T are recording sites from the dorsal, upper calcarine, lower calcarine, and tentorial surfaces, respectively. Striate cortex is shaded. Broken lines circumscribe areas of tissue shown in photomicrographs in Fig. 7. Upper right, A perimeter chart of the temporal hemifield of the right eye with receptive fields corresponding to the recording sites below. Solid receptive fields are for recording sites in striate cortex; outlined receptive fields, for area 18. Receptive fields were determined for recording sites in dorsal, tentorial, and lower calcarine juxtastriate cortex. No responses evoked by visual stimuli were recorded from upper calcarine juxtastriate cortex in penetrations 10–14.

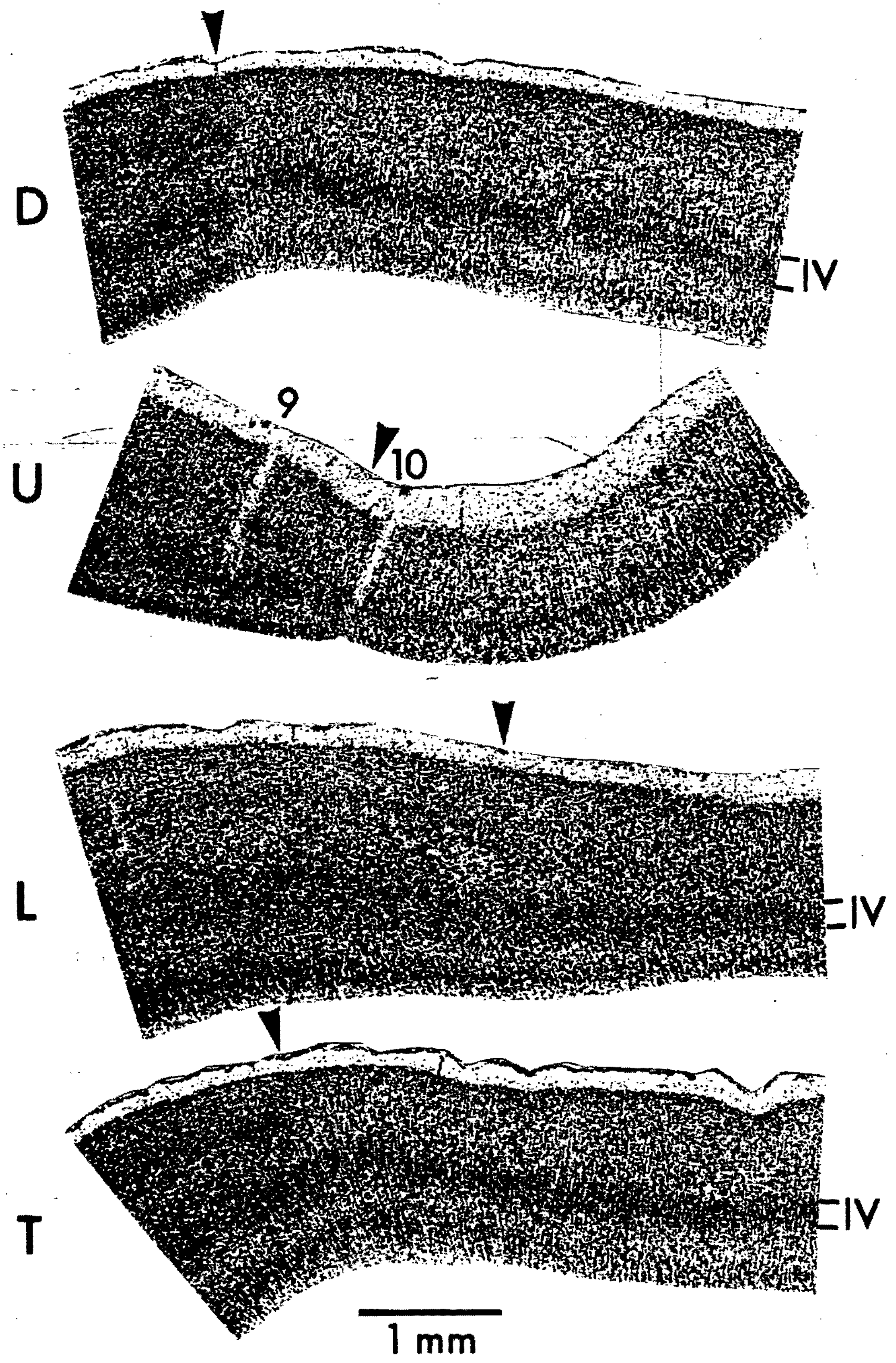


Fig. 7. Photomicrographs of the enclosed areas indicated in the parasagittal brain section of Fig. 6. Responsive juxtastriate cortex is histologically distinct from nonresponsive juxtrastriate cortex. Photomicrographs labeled D, U, L, and T are from the dorsal surface, upper calcarine, lower calcarine, and tentorial surface, respectively. Arrowheads indicate the striate border which is less apparent in L because of the angle of the section. In U, electrode tracts 9 and 10 are apparent; the remaining electrode tracts are not visible in the portions of the sections illustrated. The dense layer IV identifying cortical area 18 is marked in D, L and T, but is absent in the thinner juxtastriate cortex of U.

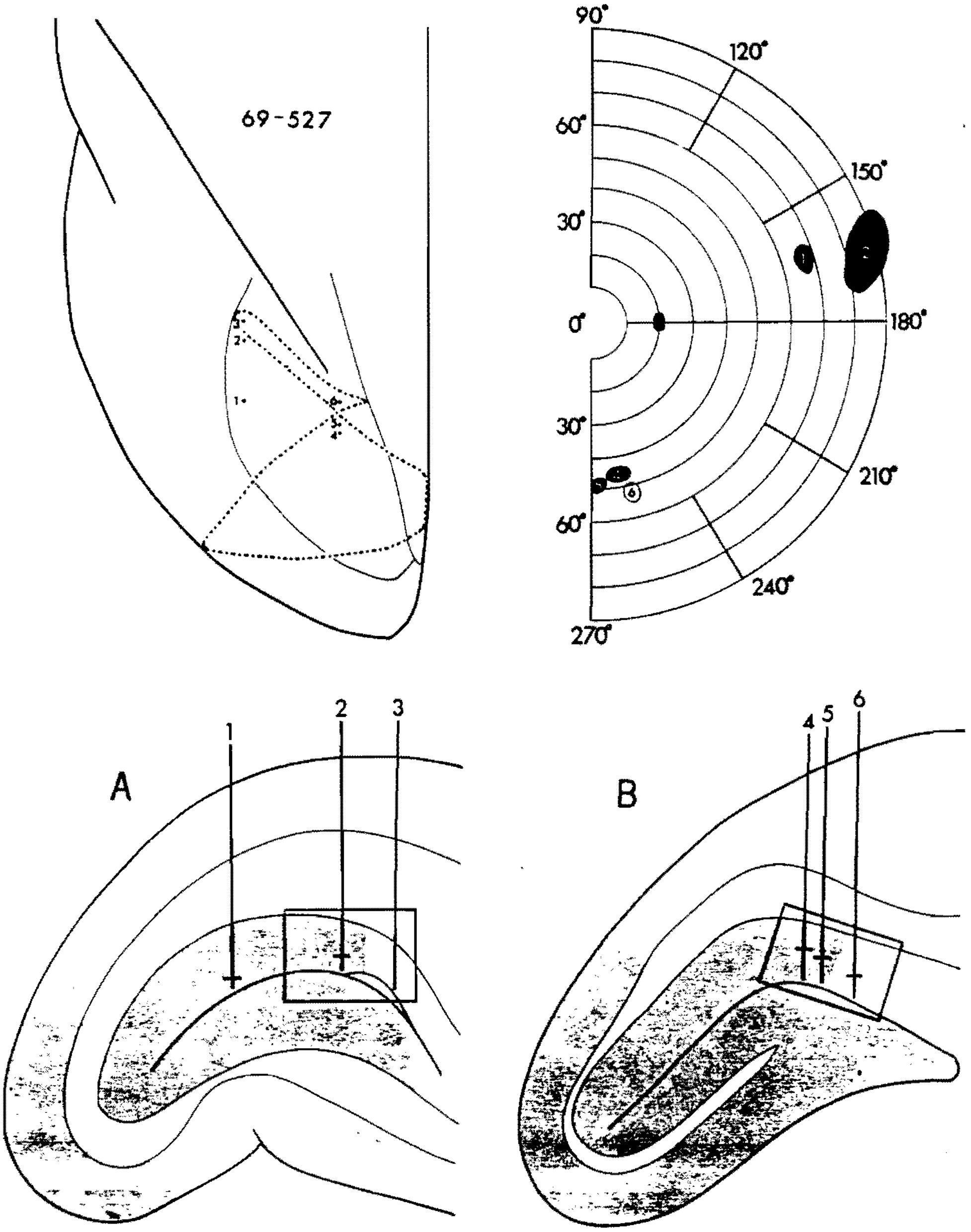


Fig. 8. Visually responsive and nonresponsive sectors of upper calcarine juxtastriate cortex. The responsive sector is adjacent to the representation of the vertical meridian in striate cortex; the nonresponsive sector is adjacent to the representation of the temporal periphery. Upper left, a dorsal view of the posterior two-thirds of the left cerebral hemisphere. As in Fig. 6, numbered dots mark vertical electrode penetrations; thin lines, the calcarine sulcus; and the broken line, the border of striate cortex. The two rows of electrode penetrations are indicated on two parasagittal brain sections below. Striate cortex is shaded and boxes enclose regions shown in photomicrographs in Fig. 9. Horizontal bars mark recording sites and the corresponding receptive fields are shown on a perimeter chart above. Penetration 3 adjacent to the striate cortex representation of the temporal periphery did not encounter neurons activated by visual stimuli on the upper bank of the calcarine sulcus while the more medial penetration 6 adjacent to the striate representation of the vertical meridian did.

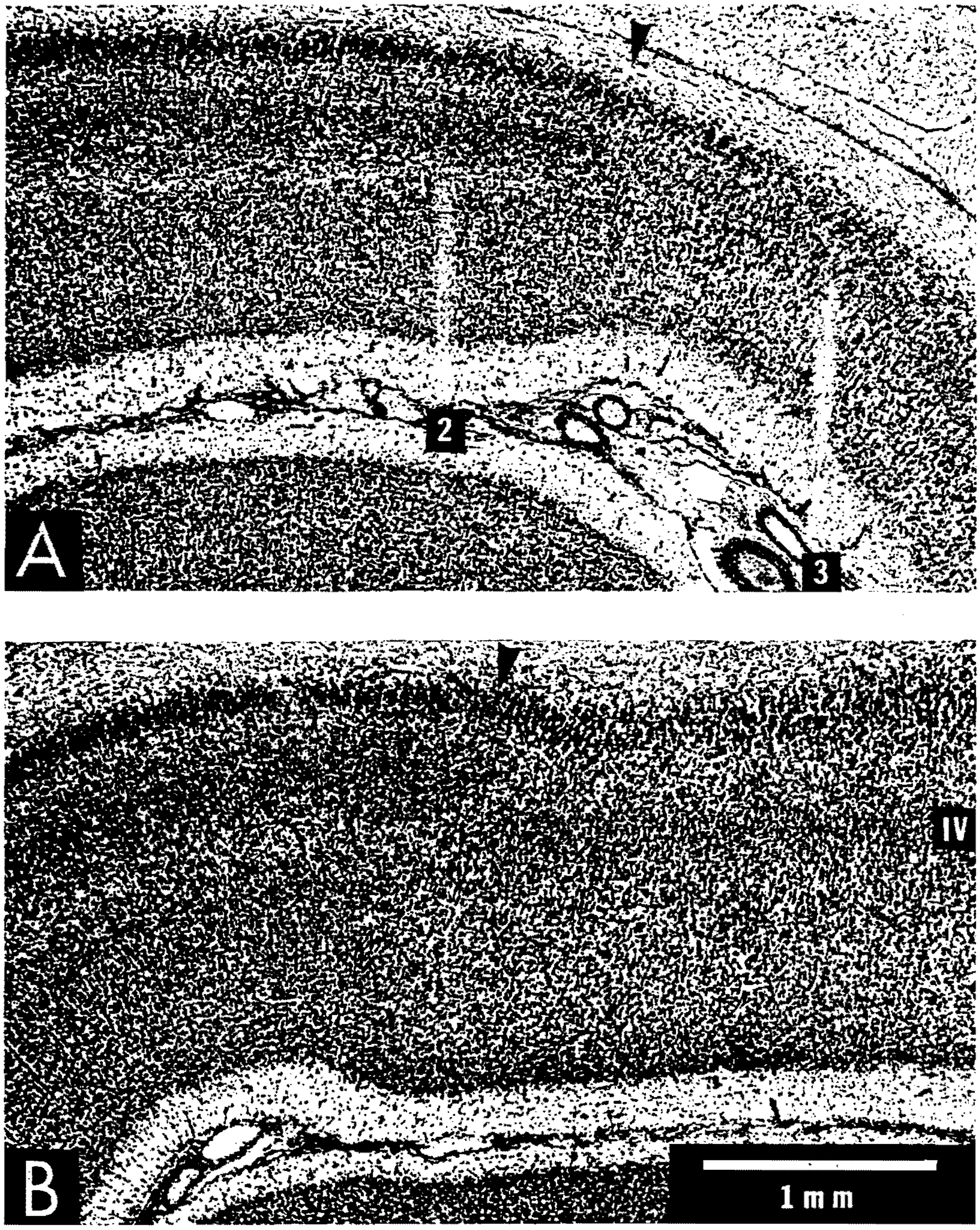


Fig. 9. Responsive (B) and nonresponsive (A) juxtastriate cortex. Photomicrographs are from the two areas of the upper bank of the calcarine sulcus enclosed in boxes in Fig. 8. Electrode tracts 2 and 3 of Fig. 8 are apparent in photomicrograph A. Penetration 3, just rostral to striate cortex, did not encounter neurons activated by visual stimuli. In B, the IV layer of cells is labeled in visually responsive area 18.

The second area did not completely surround V I. A small bordering region on the upper bank of the calcarine sulcus did not respond to visual stimuli. As is shown by the locations of penetrations 10–14 in Fig. 6 and 3 in Fig. 8, this nonresponsive bordering cortex adjoined the representation of the temporal periphery of the visual field in V I.

Cytoarchitectonics of responsive and nonresponsive adjoining cortex

The histological structure of the two types of cortex adjacent to area 17 can be seen in Fig. 7, where photomicrographs of brain sections from locations indicated in Fig. 6 are shown. In all 4 photomicrographs, striate cortex, with a broad layer IV of cells and a dense layer VI of cells, is apparent on the left. The border of striate cortex is indicated by a small arrowhead and is easily identified in photomicrographs D, U, and T, but is less apparent in L where the cortex was cut in a plane slightly oblique to the surface. To the right of the border of striate cortex, architectonic area 18, as described in the owl monkey by Hassler[9], can be identified by the dense layer IV of cells in photomicrographs D, L, and T. In photomicrograph U, the cortex bordering area 17 is quite different in structure from area 18 and corresponds to the 'prostriata' of Sanides and Vitzthum[22,29]. The cortex adjoining area 17 in photomicrograph U is much thinner than in photomicrographs D, L, and T and the IVth layer of cells is poorly developed in comparison to area 18. Electrode tracts 9 and 10 are clear in photomicrograph U and neurons at recording site 9 U in striate cortex responded to visual stimuli, while no neural responses to visual stimuli were obtained in the adjacent cortex of penetration 10. However, recording sites in area 18 were activated by visual stimuli.

Area 'prostriata' occupies a limited extent of the upper bank of the calcarine sulcus. In Fig. 9, this nonresponsive bordering area of the upper bank was identified by electrode penetrations 2 and 3. Again, visual responses were recorded in striate cortex (penetration 2) and not in adjoining area 'prostriata' (penetration 3). Somewhat more medial on the upper bank of the calcarine sulcus, visual responses were obtained in both striate and adjoining cortex and this adjoining cortex can be identified as area 18 in photomicrograph B in Fig. 9.

In summary, the evidence indicates that area 18 or V II borders the complete representation of the vertical meridian in V I. A second type of cortex which did not respond to visual stimuli borders the representation of the temporal periphery in V I. The portion of the border of V I that corresponds to the vertical meridian and the portion that corresponds to the extreme temporal periphery are shown in Fig. 5.

DISCUSSION

Striate cortex (V I)

The representation of the visual field in striate cortex of the owl monkey is similar to that of other monkeys[4,7,12,21,26] in that the center of gaze is represented on the lateral surface of the occipital lobe with the representation of the upper visual field extending onto the tentorial surface and into the calcarine fissure and the representation of the lower visual field extending onto the medial wall and into the calcarine sulcus. However, the owl monkey appears to have proportionately less striate cortex devoted to the representation of central vision than the squirrel monkey, macaque monkey or baboon. Thus the portion of the visual field extending within 15° of the center of gaze is represented on the dorsal and tentorial surfaces of the occipital lobe of the owl monkey, while only the central 2–4° of visual field are represented on the dorsal surface in squirrel monkeys[4] and 6–9° in macaque monkeys[26]. The difference in the proportion of striate cortex devoted to central vision in owl monkeys and in macaques and baboons can be seen by comparing Fig. 5 of the present paper with a similar planar representation of striate cortex in Fig. 5 of Daniel and Whitteridge[7]. The proportionately smaller representation of central vision in owl monkey correlates with the absence of the retinal fovea[32], nocturnality[18], and lower visual acuity than squirrel monkeys[19].

In the owl monkey, 90% of the striate border is devoted to the vertical meridian and only 10% to the extreme temporal periphery. These proportions are similar to the estimate of Whitteridge[31] that 95% of the striate border of macaques and baboons is devoted to the vertical meridian and 5% to the extreme temporal periphery. While the estimate of Whitteridge may be questioned, since it depends on extrapolating from the recordings from the more central portions of the striate representation as reported by Daniel and Whitteridge[7], the values appear quite reasonable when compared to those obtained for the owl monkey. Proportionately more of the striate border would be expected to represent the vertical meridian in baboons and macaques, where more cortex is devoted to central vision than in owl monkeys. On the other hand, the estimate from Polyak's Fig. 259[21] that approximately one-third of the striate border represents the temporal periphery in 'man and in other primates' is not supported by the present results.

It has been reported that the lower bank of the calcarine sulcus of monkeys represents the upper visual field and the upper bank represents the lower visual field[4,7,21]. Our data indicate that much of the peripheral portion of the upper visual field is represented on the *upper* bank of the calcarine sulcus in the owl monkey. The location of the representation of the upper visual field may be similar in other monkeys and it is possible to argue by extrapolating from the relations of receptive fields and recording sites in Fig. 4 of Cowey's report[4] that even more of the peripheral portion of the upper visual field is represented on the upper bank of the calcarine sulcus in squirrel monkeys than in owl monkeys.

In the present report, we attempted to illustrate the representation of the visual field in the unfolded striate cortex of the owl monkey (see Fig. 5). This illustration of striate cortex as half of a distorted ellipsoid larger at one end than the other is similar to that given for Old World monkeys by Polyak[21] and Daniel and Whitteridge[7]. In indicating that the center of gaze is represented at the larger end of the ellipsoid, our illustration corresponds to that of Polyak[21], but differs from that of Daniel and Whitteridge[7].

Bordering cortex: areas 18 and 'prostriata'

The results of the present study suggest that at least two distinct types of cortex border striate cortex. One type, architectonic area 18, borders 90% of striate cortex and extends from the dorsal surface onto the medial wall, the tentorial surface and both banks of the calcarine fissure. In area 18, neurons respond to visual stimuli and the area is visuotopically organized. On the dorsal surface, receptive fields for rows of recording sites that proceed rostrally away from striate cortex correspond to rows of receptive fields that proceed away from the vertical meridian towards the temporal periphery of the contralateral hemifield and toward the horizontal meridian. This result is in agreement with the electrophysiological report of Cowey[4] on squirrel monkeys and the observations of Hubel and Wiesel on macaque monkeys[13]. This result also is supported by the conclusions of the fiber degeneration studies of Spatz, Tigges and Tigges[24] on squirrel monkeys and Kuypers *et al.*[16], Zeki[35] and Cragg and Ainsworth[5] on macaque monkeys. These investigators found that striate cortex projects to area 18 in a topographical pattern. Lesions near the striate border produced terminal degenerations in closely adjacent portions of area 18, while more caudal lesions in area 17 produced degeneration in more rostral portions of area 18. In a single electrophysiological experiment, we obtained results similar to those in the owl monkey for recording sites in area 18 of the lunate sulcus of a rhesus monkey. Successive receptive fields for rows of recording sites proceeding away from striate cortex down the bank of the lunate sulcus progressed temporally away from the vertical meridian and toward the horizontal meridian of the contralateral half of the visual field.

In addition to area 18 of the dorsal surface, successions of receptive fields also progress away from the vertical meridian into the temporal hemifield for rows of recording sites proceeding away from striate cortex in area 18 of the tentorial surface, medial wall and both banks of the calcarine sulcus. Thus, the second visual area, V II, is coextensive with the complete length of area 18. Except for the portion of area 18 adjoining area 17 of the dorsal surface of the occipital lobe, this result previously had not been supported by direct electrophysiological evidence. Cowey[4] was unable to activate cortex bordering area 17 on the medial wall of the squirrel monkey with visual stimuli and visual responses were not obtained at all in area 18 of rhesus monkeys by Cowey[4] and by Daniel and Whitteridge[7].

Our evidence also indicates that in the owl monkey V II borders only the representation of the vertical meridian of V I. This result corresponds to the earlier suggestions of Woolsey[33], Thompson, Woolsey and Talbot[28] and Whitteridge[30]. These investigators reasoned that if V II bordered V I along the representation of the vertical median in cats[25] and rabbits[28], then the same relationship should exist in monkeys. Recent evidence suggests that V II also borders V I only along the representation of the vertical meridian in hedgehogs[14], tree shrews[15] and squirrels[8].

In the present report, a small zone of cortex adjoining area 17 was found to be nonresponsive to visual stimuli with our recording conditions. This cortex adjoins the representation of the temporal periphery of the contralateral hemifield in striate cortex on the rostral upper bank of the calcarine fissure and forms about 10% of the border of striate cortex. The nonresponsive cortex is thinner than striate cortex or area 18 and cortical layers III and IV are poorly developed. A corresponding region in man, chimpanzee, and cat, has been termed 'prostriata'[22,23,29]. The nonresponsive region in the owl monkey also appears to correspond to a juxtastriate area of cortex in the upper bank of the calcarine fissure of squirrel monkeys termed retrosplenial cortex in the report of Cuénod *et al.*[6]. However, these investigators found neurons in this cortical area of the squirrel monkey which were responsive to a brief intense flash of light. While we do not suggest that 'prostriata' would be nonresponsive to visual stimuli with all recording conditions, the cortex bordering the representation of the temporal periphery of the contralateral hemifield in striate cortex was found nonresponsive in the hedgehog[14], grey squirrel[8], and tree shrew[15] during recording conditions similar to those used for the owl monkeys of the present report. Evidence for visual input into caudal 'limbic' cortex has been reviewed by MacLean[17] and Woolsey[34].

SUMMARY

Microelectrode mapping methods were used to determine the representation of the visual field in striate cortex and adjacent cortex in the owl monkey. As in other primates, the center of gaze is represented in dorsolateral striate cortex. Most of the lower quadrant of the visual field is represented on the upper bank of the calcarine sulcus, while more central portions of the lower quadrant are represented on the medial wall and dorsal surface. The representation of the upper quadrant extends from the dorsolateral surface over the tentorial surface and across the lower bank of the calcarine sulcus. The representation of the temporal periphery of the upper quadrant was found on the upper bank of the calcarine sulcus. Almost half of striate cortex is devoted to the central 20° of the visual field and 90% of the border corresponds to the zero vertical meridian or line of decussation.

Recordings from cortex adjoining striate cortex indicate that the second visual area, V II, borders the complete vertical meridian of striate cortex. The small representation of the temporal periphery in striate cortex is bordered by cortex that was nonresponsive to visual stimuli. The responsive and nonresponsive bordering areas were found to relate to two histologically distinct types of cortex, areas 18 and 'prostriata', respectively.

ACKNOWLEDGEMENTS

This study was supported by Grant 5-P01-NS-06225 to the Laboratory of Neurophysiology, University of Wisconsin. J. M. Allman was a National Science Foundation Predoctoral Fellow in the Department of Anthropology, University of Chicago. J. H. Kaas was supported by 1-P01-HD-03352.

We thank Dr. Leon Schmidt, Southern Research Institute, Birmingham, Alabama, for providing the owl monkeys used in this study. We also thank Drs. C. N. Woolsey, R. M. Benjamin and R. W. Guillery for helpful comments on the manuscript. Histological materials were prepared by Mrs. Jo Ann Ekleberry and Mrs. Isabel Lucey. Photographic work was done by Mr. T. P. Stewart.

REFERENCES

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

2 Brindley, G. S., and Lewin, W. S., The sensations produced by electrical stimulation of the visual cortex, *J. Physiol. (Lond.)*, 196 (1968) 479–493.

3 Brouwer, B., and Zeeman, W. P. C., The projection of the retina in the primary optic neuron in monkeys, *Brain*, 49 (1926) 1–35.

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

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

6 Cuénod, M., Casey, K. L., and MacLean, P. D., Unit analysis of visual input to posterior limbic cortex I. Photic stimulation, *J. Neurophysiol.*, 28 (1965) 1101–1117.

7 Daniel, P. M., and Whitteridge, D., The representation of the visual field on the cerebral cortex in monkeys, *J. Physiol. (Lond.)*, 159 (1961) 203–221.

8 Hall, W. C., Kaas, J. H., Killackey, H., and Diamond, I. T., Cortical visual area in the grey squirrel (*Sciurus carolinesis*): a correlation between cortical evoked potential maps and architectonic subdivisions, *J. Neurophysiol.*, 34 (1971) 437–452.

9 Hassler, R., Comparative anatomy of the central visual systems in day- and night-active primates. In R. Hassler and H. Stephan (Eds.), *Evolution of the Forebrain*, Plenum Press, New York, 1967, pp. 419–434.

10 Holmes, G., Disturbances of vision by cerebral lesions, *J. Physiol. (Lond.)*, 160 (1962) 106–154.

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

12 Hubel, D. H., and Wiesel, T. N., Receptive fields and functional architecture of monkey striate cortex, *J. Physiol. (Lond.)*, 195 (1968) 215–243.

13 Hubel, D. H., and Wiesel, T. N., Cells sensitive to binocular depth in area 18 of the macaque monkey cortex, *Nature (Lond.)*, 225 (1970) 41–42.

14 Kaas, J. H., Hall, W. C., and Diamond, I. T., Cortical visual areas I and II in the hedgehog: the relation between evoked potential maps and architectonic subdivisions, *J. Neurophysiol.*, 33 (1970) 595–615.

15 Kaas, J. H., Killackey, H., Hall, W. C., and Diamond, I. T., Cortical visual areas in the tree shrew (*Tupaia glis*), in preparation.

16 Kuypers, H. G. J. M., Szwarcbart, M. K., Mishkin, M., and Rosvold, H. E., Occipitotemporal cortico-cortical connections in the rhesus monkey, *Exp. Neurol.*, 11 (1965) 245–262.

17 MacLean, P. D., The limbic and visual cortex in phylogeny: further insights from anatomic and microelectrode studies. In R. Hassler and H. Stephan (Eds.), *Evolution of the Forebrain*, Plenum Press, New York, 1967, pp. 443–453.

18 Moynihan, M., *Some Behavior Patterns of Platyrrhine Monkeys. I. The Night Monkey (Aotus trivirgatus)*, Smithsonian Institution, Washington, 1964, pp. 1–84.

19 Ordy, J. M., and Samorajski, T., Visual acuity and ERG–CFF in relation to the morphologic organization of the retina among diurnal and nocturnal primates, *Vision Res.*, 8 (1968) 1205–1225.

20 Polyak, S., *The Main Afferent Fiber Systems of the Cerebral Cortex in Primates*, Univ. California Press, Berkeley, 1932, pp. 1–370.

21 Polyak, S., *The Vertebrate Visual System*, Univ. of Chicago Press, Chicago, 1957, pp. 1–1390.

22 Sanides, F., Functional architecture of motor and sensory cortices in primates in light of a new concept of neocortical evolution. In C. R. Noback and W. Montagna (Eds.), *The Primate Brain*, Appleton-Century-Crofts, New York, 1970, pp. 137–208.

23 Sanides, F., and Hoffmann, J., Cyto-and myeloarchitecture of the visual cortex and surrounding association areas in the cat, *J. Hirnforsch.*, 11 (1969) 79–104.

24 Spatz, W. B., Tigges, J., and Tigges, M., Subcortical projections, cortical associations, and some intrinsic interlaminar connections of the striate cortex in the squirrel monkey (*Saimiri*), *J. comp. Neurol.*, 140 (1970) 155–174.

25 Talbot, S. A., A lateral localization in cat's visual cortex, *Fed. Proc.*, 1 (1941) 84.

26 Talbot, S. A., and Marshall, W. H., Physiological studies of neural mechanisms of visual localization and discrimination, *Amer. J. Ophthal.*, 24 (1941) 1255–1264.

27 Teuber, H. L., Battersby, W. S., and Bender, M. B., *Visual Field Defects after Penetrating Missile Wounds of the Brain*, Harvard Univ. Press, Cambridge, 1960, pp. 1–143.

28 Thompson, J. M., Woolsey, C. N., and Talbot, S. A., Visual areas I and II of cerebral cortex of rabbit, *J. Neurophysiol.*, 12 (1950) 277–288.

29 Vitzthum, H. G. von, und Sanides, F., Entwicklungsprinzipien der menschlichen Sehrinde. In R. Hassler and H. Stephen (Eds.), *Evolution of the Forebrain*, Plenum Press, New York, 1967, pp. 435–442.

30 Whitteridge, D., Area 18 and the vertical meridian of the visual field. In E. G. Ettlinger (Ed.), *Functions of the Corpus Callosum*, Churchill, London, 1965, pp. 115–120.

31 Whitteridge, D., Geometrical relations between the retina and the visual cortex. In *Mathematics and Computer Science in Biology and Medicine*, H. M. Stationery Office, London, 1965, pp. 269–277.

32 Wolin, L. R., and Massopust, L. C., Morphology of the primate retina. In C. R. Noback and W. Montagna (Eds.), *The Primate Brain*, Appleton-Century-Crofts, New York, 1970, pp. 1–27.

33 Woolsey, C. N., The somatic functions of the central nervous system, *Ann. Rev. Physiol.*, 9 (1947) 525–552.

34 Woolsey, C. N., Comparative studies on cortical representation of vision, *Vision Res.*, Suppl. 3 (1971) in press.

35 Zeki, S. M., The secondary visual areas of the monkey, *Brain Research*, 13 (1969) 197–226.

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