Brain Research, 100 (1975) 473–487
© Elsevier Scientific Publishing Company, Amsterdam – Printed in The Netherlands

Research Reports

THE DORSOMEDIAL CORTICAL VISUAL AREA: A THIRD TIER AREA IN THE OCCIPITAL LOBE OF THE OWL MONKEY *(AOTUS TRIVIRGATUS)*

J. M. ALLMAN AND J. H. KAAS

Division of Biology, 216-76 Beckman Laboratories, California Institute of Technology, Pasadena, Calif. 91125, Department of Psychology, Vanderbilt University, Nashville, Tenn. 37240 and Department of Neurophysiology, University of Wisconsin, Madison, Wisc. 53706 (U.S.A.)

(Accepted June 30th, 1975)

SUMMARY

In the owl monkey, microelectrode mapping of Brodmann's area 19 indicates that this region contains part or all of at least 5 separate representations of the visual field, each of which adjoins the anterior border of V II and collectively are termed the *third tier* of cortical visual areas (V I is the first tier; V II is the second tier). Described in detail in this report is one of the third tier areas which is located on the dorsal surface and the adjacent medial wall of the occipital lobe and corresponds to a densely myelinated zone of cortex. In this dorsomedial area (DM), the representation of the horizontal meridian is partially split, and thus, like V II (see ref. 4) and the dorsolateral crescent[5], DM is a second order transformation of the visual hemifield.

In one abnormal owl monkey, a portion of the upper quadrant was represented twice in DM. This abnormal case may provide some clues as to how the normal pattern of visuotopic organization is established in the developing brain.

INTRODUCTION

The traditional view of the organization of the visual cortex in primates, stemming from the cytoarchitectonic observations of Brodmann[8–10], is that there exists a primary visual cortex, area 17, which is completely surrounded by two concentric zones, area 18 and area 19 (see Fig. 1). In recent years, microelectrode mapping studies[1–6] and investigations of the connections of the visual areas[11,12,18,19,21–23,25,26] have provided additional information concerning the organization of visual cortex that may be compared with the Brodmann scheme of concentric areas. In our contributions to this endeavor, we have used mainly a small New World primate, the owl monkey (*Aotus trivirgatus*), because the cerebral cortex in this species is much less convoluted than in most simian primates. In Fig. 2 the owl monkey's visual cortex is presented in an unfolded format to illustrate the representations of the visual field as revealed by our experiments to date.

In all primates area 17 corresponds to a topological representation of the contralateral half of the visual field, V I (see ref. 2 for a review). The representation is divided into upper and lower quadrants by the horizontal meridian. Nearly all of the border of V I is devoted to the representation of the vertical meridian. The small remaining portion of the V I border is devoted to the representation of the extreme temporal periphery of the contralateral visual hemifield and lies deeply buried in the calcarine sulcus. The primary visual area is nearly surrounded by a second representation of the contralateral visual hemifield, the second visual area or V II (see ref. 2 for review). The representation of the vertical meridian forms the common border between V I and V II, and therefore V II does not completely surround V I. The representation of the periphery in V I is not adjoined by V II but instead is bordered by a distinct architectonic zone, the *area prostriata* of Sanides[20]. Most of the outer boundary of V II is formed by the horizontal meridian, and V II appears to correspond with most of area 18 as identified by Brodmann in New World monkeys and prosimians[9,10]. Detailed electrophysiological maps of V II in Old World monkeys are not yet available, but anatomical studies of the connections of V I[12,26] indicate that Brodmann[8,10] designated a wider belt of cortex as area 18 in Old World monkeys and that this wider belt includes more visual cortex than just V II. By extension, it is probable that Brodmann's[10] portrayal of area 18 in man includes more than V II.

In a non-primate, the cat, microelectrode recordings indicate that a third visual area (V III) corresponds to area 19 and possesses a visuotopic organization that is approximately the mirror image of the adjacent V II[14,24]. However, in two primates, a prosimian, (*Galago senegalensis*) and the owl monkey, we have found that the cortex corresponding to area 19 contains more than one representation of the visual field. In the primate in which this region has been most fully explored, the owl monkey, there exist at least 5 distinct representations of the visual field that adjoin the anterior border of V II. These areas include the dorsolateral crescent (DL), the dorsomedial (DM), the medial (M), the dorsointermediate (DI) which has not yet been mapped in detail, and a tentorial area which adjoins V II on the ventral surface of the occipital lobe and has also not been mapped in detail and is not shown in Fig. 2. Collectively, we refer to these representations as the *third tier* of cortical visual area (V I is the first tier; V II is the second tier). While these third tier areas approximate a band of tissue that in a very rough way may be compared to area 19 of Brodmann, each of the separate third tier areas has its own shape and distinctive histological features.

The main purpose of this report is to present evidence for one of these *third tier* areas, the dorsomedial (DM). It was some of this evidence which first led us to reconsider the traditional view of the organization of visual cortex in primates. A second purpose of this report is to illustrate data from a single owl monkey in which the visuotopic organization of DM differed markedly from the normal pattern found in other monkeys. This single abnormal case may provide some clues as to how the normal

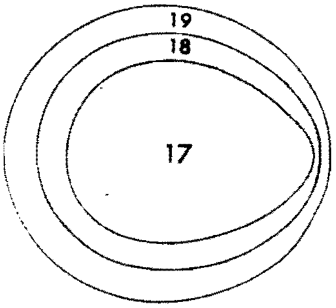

Fig. 1. A schematic unfolding of Brodmann's cytoarchitectonic areas 17, 18, and 19 in primates. Brodmann found that the relative proportions of area 17, 18, and 19 varied from species to species. This figure is intended merely to show graphically Brodmann's concept of area 17 surrounded by two concentric zones, areas 18 and 19.

pattern of visuotopic organization is established in the developing brain. In addition, such cases of differing cortical organization may account for some of the individual differences in perceptual and cognitive capacities so evident in man.

An abstract of some of the findings for DM has been published previously[6].

METHODS

The experimental procedures have been described previously[1]. The visuotopic organization of the dorsomedial visual area (DM) was explored extensively with electrophysiological mapping methods in 13 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. Tungsten and platinum–iridium microelectrodes were used to record from small clusters of neurons or occasionally from single neurons in the 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 usually covered with an opaque shield. At some recording sites, electrolytic microlesions were made by the passage of direct-current (cathodal, 20 μA for 10 sec). After recording, the animals were perfused with formol–saline, and the brains were removed, dehydrated, and embedded in celloidin. Alternate series of 30-μm sections were stained with thionin for cell bodies or hematoxylin for myelin (Heidenhain–Woelcke technique). Electrode tracks and recording sites were located in the histological sections and related to receptive field organization and cyto- and myeloarchitectonic structure.

RESULTS

Visuotopic organization of DM

Fig. 3 illustrates some of the data from an early experiment which first led us to question the concept that a single visual area, V III, adjoined the anterior border of V II. A row of recording sites started in V I, extended across V II and continued across most of the width of what we expected to be V III. The receptive field locations for the

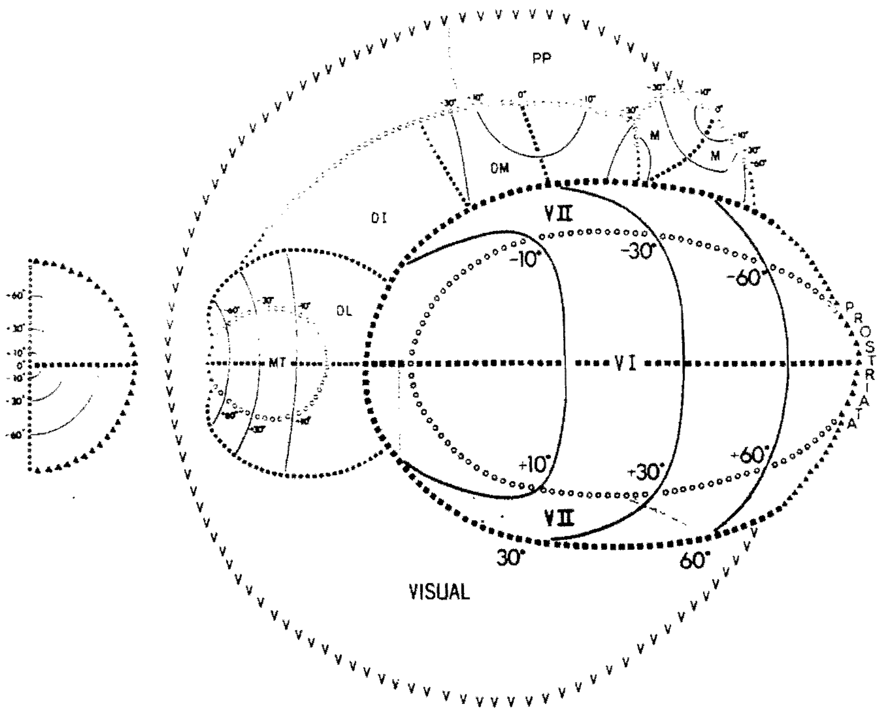

Fig. 2. A schematic unfolding of the visual cortex of the left hemisphere in the owl monkey. The visual cortex corresponds to approximately the posterior third of the entire neocortex. The unfolded visual cortex is approximately a hemispherical surface, which is viewed from above in this diagram. Data supporting this summary are contained in this paper and in refs. 1–5. The perimeter chart on the left shows the contralateral (right) half of the visual field. The circles indicate the vertical meridian, the solid squares the horizontal meridian, and the solid triangles the temporal periphery of the contralateral half of the visual field, V I, first visual area (area 17 of Brodmann); V II, second visual area; DL, dorsolateral crescent; MT, middle temporal area; DI, dorsointermediate area; DM, dorsomedial area; M, medial area; and PP, posterior parietal cortex. The row of V's indicates the outer boundary of visual cortex. The areas marked 'visual' contain additional visual representations, but these regions have not yet been mapped in detail.

recording sites were as anticipated for V I (area 17) and V II (area 18). That is, for the posterior to anterior row of recording sites, receptive fields 1 and 2 for V I moved toward the vertical meridian in the lower visual quadrant while receptive fields 3–6 for V II proceeded from the vertical meridian to the horizontal meridian in the lower visual quadrant. Since the organization of V III as described in the cat[14] is a mirror reversal of that found in V II, we expected the receptive fields for recording sites 7–10 in Fig. 3 to retrace the progression 3–6 and move from the horizontal meridian in the lower visual quadrant to the vertical meridian a few degrees below gaze. Instead, the receptive fields 7–10 extend across some 30° of the upper vertical quadrant to end near the vertical meridian. The finding of receptive fields in the upper visual quadrant next to the representation of the lower visual quadrant was clearly inconsistent with the concept of V III as a visual belt organized as a mirror reversal of V II.

Additional and more detailed experiments indicated that the receptive fields in the upper visual quadrant in Fig. 3 were part of a representation of the contralateral

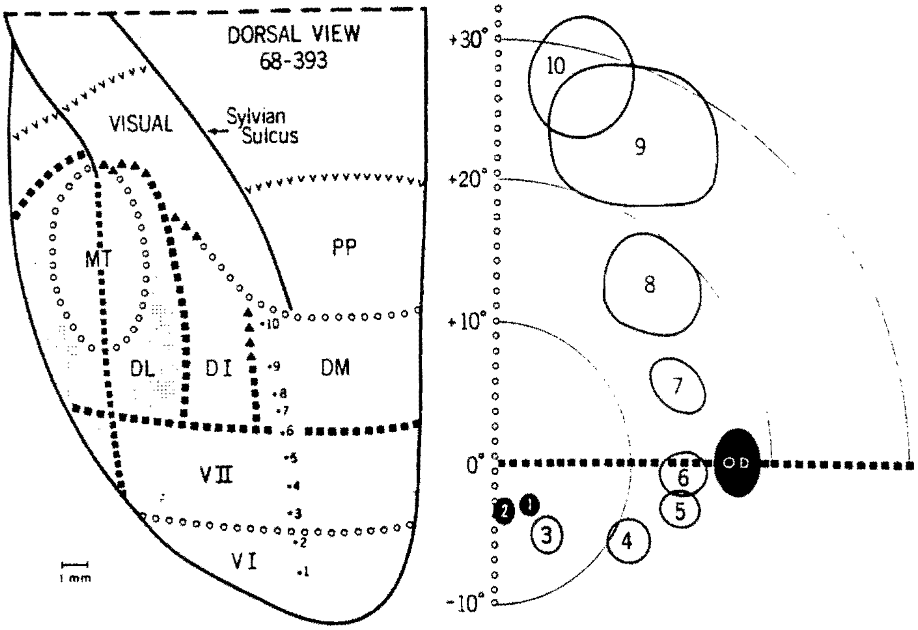

Fig. 3. Receptive fields for a row of points through V I, V II and DM in owl monkey 68-393. The diagram on the right is a line drawing of a dorsal view of the posterior two-thirds of the left cerebral hemisphere. Posterior is down; medial is to the right. V II on the dorsal view of the brain, and the receptive fields recorded from V II are shaded. The other visuotopic organization shown in this figure is based on data obtained in subsequent experiments. All conventions and abbreviations are the same as in Fig. 2.

visual field in cortex occupying only part of the anterior border of V II. The results of one of these experiments is illustrated in Fig. 4. The vertical meridian is represented along the anterior border of the area as is demonstrated by the receptive fields for recording sites 1–3, 7–9 and 10A–D. The center of gaze, which lies at the intersection of the vertical and the horizontal meridians, is represented near recording site 8. From there the horizontal meridian extends posteriorly between recording sites 14 and 15 and between 21 and 22. When the representation of the horizontal meridian reaches the posterior border of DM, at approximately 15° from the center of gaze, the horizontal meridian splits as it proceeds peripherally in the visual field and goes on to form the posterior and ventromedial border of DM, which adjoin V II, and the posterior part of the lateral border of DM, which adjoins another third tier area, the dorsointermediate (DI). Relatively peripheral receptive fields in the upper quadrant of the contralateral visual hemifield are located further anterior near the DM-DI border (see recording sites and receptive fields 1 and 4).

A further experiment shows that the more peripheral part of the lower visual quadrant is represented in about 1 mm of cortex on the medial wall of the cerebral hemisphere at the anterior border of DM. In the experiment illustrated in Fig. 5, 3 electrode penetrations extend from the dorsal surface of the left cerebral hemisphere down the cortex of the medial wall. Penetration 1 parallels the anterior border of DM and receptive fields for recording sites in this penetration move down along the vertical meridian and then extend across the periphery of the lower quadrant. The most ventral

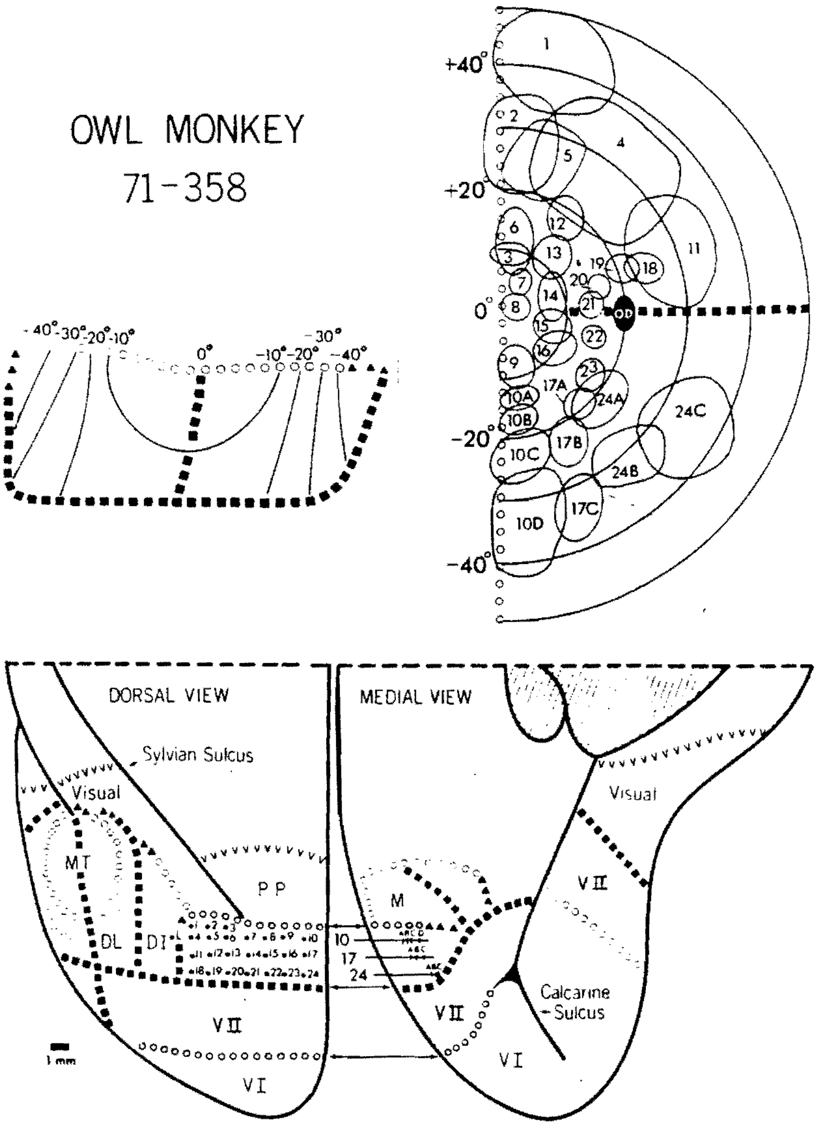

Fig. 4. The receptive field organization of the dorsomedial area in owl monkey 71-358. Tangential penetrations 10, 17 and 24 proceed parallel to the cortical surface on the medial wall of the hemisphere. The lower diagrams are dorsal and medial views of the posterior two-thirds of the left cerebral hemisphere. Posterior is down in these diagrams. The diagram on the upper left illustrates the visuotopic organization of DM plotted on a flat surface. The maps of other areas shown in this figure were obtained from other animals. All conventions and abbreviations are the same as in Fig. 2.

recording site in DM is near the V II border, and the corresponding receptive field is on the horizontal meridian. The receptive fields for penetrations 2 and 3 are less peripheral in the lower visual quadrant, and they also proceed toward the horizontal meridian with deeper recording sites nearer the V II border.

Other recordings indicate that anterior to DM another third tier visual area, the medial area (M), lies on the medial wall and shares a common border with DM in which the distal portion of the lower vertical meridian and the periphery of the lower visual quadrant are represented.

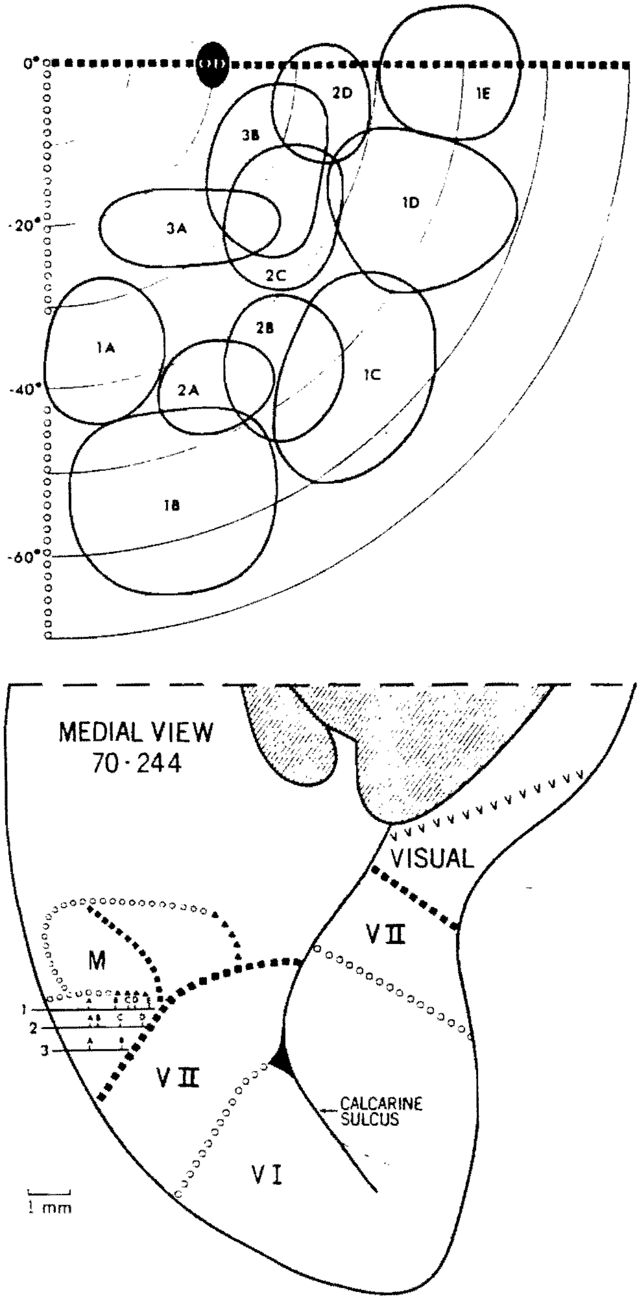

Fig. 5. The receptive field organization of DM on the medial wall of the hemisphere in owl monkey 70-244. Tangential penetrations 1, 2 and 3 proceed in parallel to the cortical surface on the medial wall. The maps of other areas shown in this figure were obtained from other animals. All conventions and abbreviations are the same as in Figs. 2–4.

Histological structure of DM

The most distinctive histological feature of DM is the heavy myelination of the deeper cortical layers. This is illustrated in the upper half of Fig. 6, which is a photomicrograph of a coronal section through DM stained with hematoxylin for myelin. The microlesion 'L' was made during the course of the experiment illustrated in Fig. 4

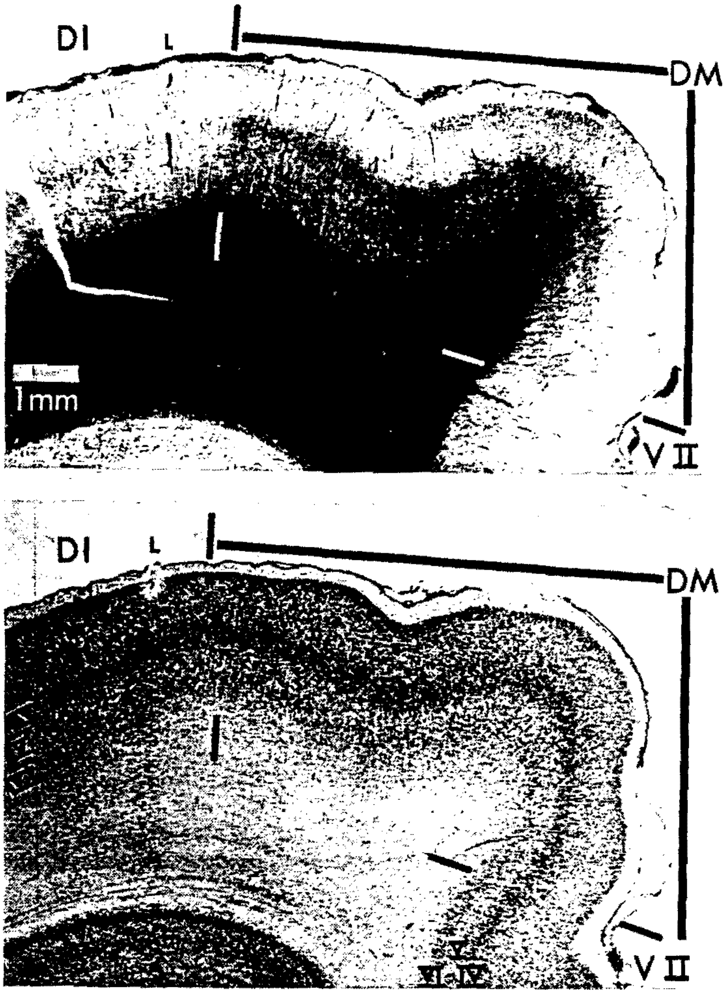

Fig. 6. Photomicrographs of adjacent 30 μm coronal sections through DM and adjacent areas from owl monkey 71-358. The upper section is stained with hematoxylin for myelinated axons; the lower section is stained with thionin for neuron cell bodies. 'L' indicates the site of an electrolytic microlesion. Roman numerals IV, V and VI denote cortical laminae in cell stain.

to mark a site just beyond the lateral border of DM as determined by a change in visuotopic organization. The lesion site also lies just beyond the lateral border of DM as revealed by histological criteria. The lower half of Fig. 6 is a photomicrograph of an adjacent section stained with thionin for the cell bodies of neurons. Although it is not so obvious as in the myelin stain, several consistent cytoarchitectonic features distinguish DM from two adjacent cortical areas. Comparing DM to V II, DM possesses a relatively wider and more densely cellular layer IV and a sparsely packed and indistinct layer VI. Comparing DM to DI, the cells in layer V of DM are much less densely packed than in DI, which causes layer V in DM to stand out as a white band in the cell stain.

A case of abnormal visuotopic organization in DM

The results from one experiment revealed a visuotopic organization that is dramatically different from all the other 9 monkeys in which we mapped the comparable region of DM on the medial wall of the hemisphere. Because of the surprising nature of these results, we remapped many of the penetrations in both the normal and the abnormal segments of DM in this animal and obtained the same receptive fields as we had previously. Furthermore, we checked the projection of the optic disc onto the plastic hemisphere and found it also was unchanged. These results, which indicate that occasionally cortical visual areas develop aberrantly, are illustrated in Fig. 7. As compared with other owl monkeys, the positions of the receptive fields for penetrations 1 through 8 in experiment 71-185 occupy approximately their normal locations in the upper quadrant and near the center in the lower quadrant. However, only 0.5 mm medial to penetration 8, abnormal organization is revealed by penetration 9. Neurons in the location of penetration 9 in DM would normally have receptive fields well into the lower quadrant, but in this case the receptive field was actually more than 20° *above* the horizontal meridian in the *upper* quadrant. Penetrations 10 and 11 extend parallel to the cortical surface down the medial wall of the hemisphere through additional abnormal cortex representing the upper quadrant. The abnormally located receptive fields in penetration 10 extend in the upper quadrant from near the vertical meridian to near the horizontal meridian in the far periphery. The normal progression of receptive fields for this portion of DM is to extend in the lower quadrant from near the vertical meridian to near the horizontal meridian in the periphery (see penetrations 1 and 2, Fig. 5). Thus, penetration 10 in the abnormal segment of DM has a receptive field progression that is approximately the mirror image about the horizontal meridian of the normal receptive field progression in this part of DM. Likewise, if penetration 11 through the abnormal segment of DM is compared with the similarly located penetration 3 in Fig. 5, it can be seen that this abnormal progression in the upper quadrant is a mirror image about the horizontal meridian of the normal progression in the lower quadrant. Thus, *the receptive fields of neurons in the abnormal segment of DM are located approximately the normal distance from the vertical and horizontal meridians appropriate for their positions within the visuotopic map of DM but are located in the wrong quadrant.*

Continuing penetration 10 into V II just below the abnormal segment of DM, receptive fields 10E through 10H proceed in the lower quadrant from the horizontal meridian toward the vertical meridian and agree closely with the receptive field organization obtained for this portion of V II in previous experiments (see Allman and Kaas[4], Fig. 4). Since these normal receptive fields for penetration 10 in V II occupy the same portion of the visual field as would normally be represented in the adjacent abnormal segment of V II, it appears that the abnormality may have been limited to DM, although no additional cortical visual areas were checked for the abnormality. It is striking that the abnormal segment of DM has quite discrete borders as defined by receptive field mapping; however we were unable to find any comparable abnormality in the histological structure of this region of DM in this animal.

Response properties of neurons in DM

A quantitative study of the properties of single neurons in DM is in progress. It

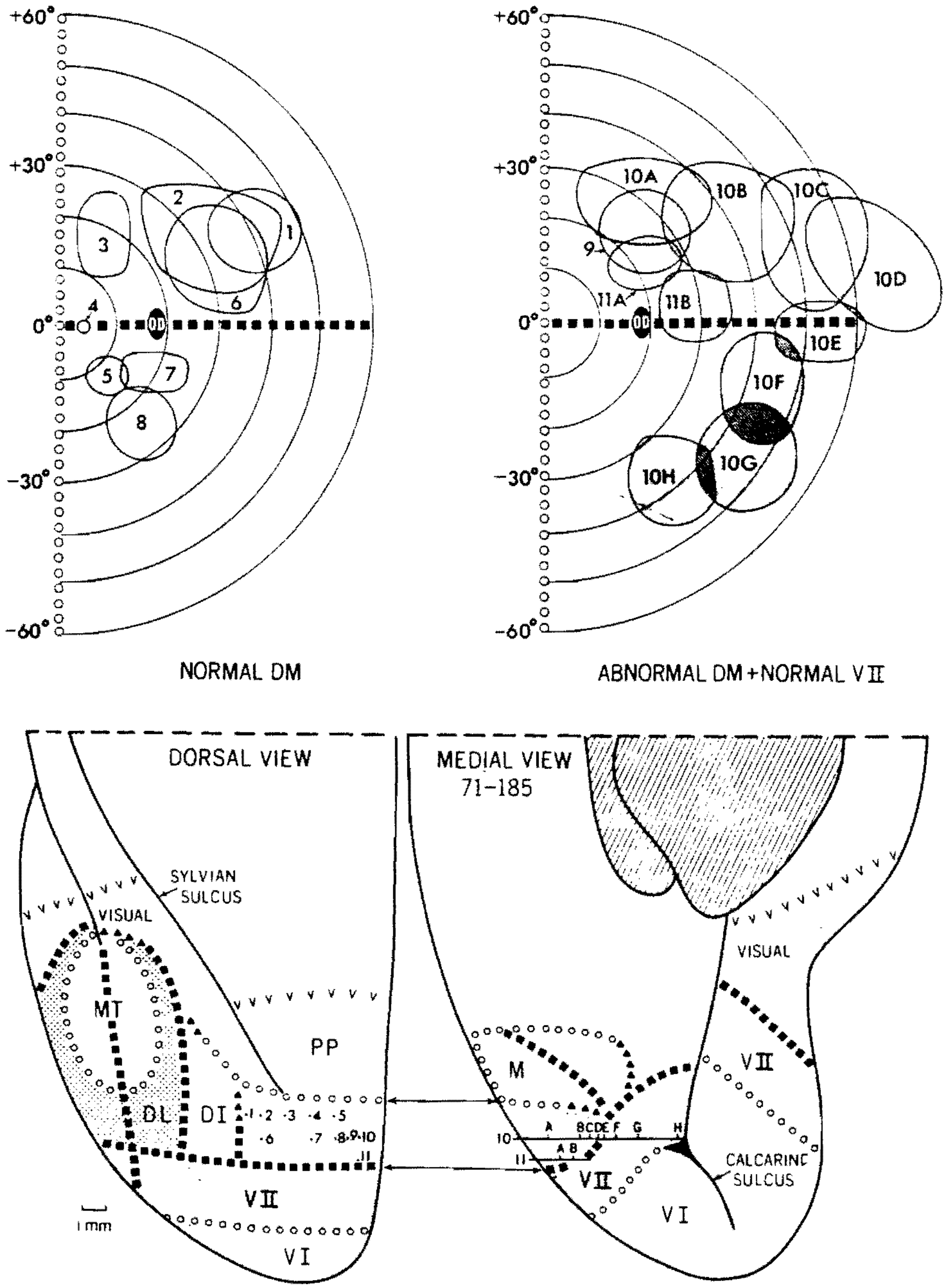

Fig. 7. Abnormal receptive field organization in DM together with adjacent normal DM and V II in owl monkey 71-185. The abnormal segment of DM in the dorsal and medial views of the brain and the corresponding abnormal receptive fields are lightly shaded. V II on the dorsal and medial views of the brain, and the receptive fields recorded from V II are more darkly shaded. The normal visuotopic organization shown for other areas are based on data obtained from other experiments. All conventions and abbreviations are the same as in Figs. 2–5.

would be premature to elaborate on the findings of this study; however, a few observations can be made. As for other areas of visual cortex, bars of light or shadow are effective stimuli when moving but not when stationary. Some neurons were orientation selective while others preferred stimuli moving in a particular direction. In several instances, dramatic binocular facilitation has been observed. Most interesting, however, is the observation that many neurons appear to be fairly sharply tuned for the velocity of stimulus movement.

The responses of neurons in the abnormal segment of DM in owl monkey 71-185 were much more vigorous than normal, which suggests an absence of normal inhibitory inputs.

DISCUSSION

The results indicate that there is a representation of the visual hemifield in a small wedge of dorsomedial occipital cortex along part of the anterior border of V II in the owl monkey. The area can be histologically distinguished from adjoining areas by its heavy myelination. Because of its location, we have called the representation the dorsomedial visual area (DM).

DM and the concept of area 19 as a third visual area (V III)

The dorsomedial area is in part of the visual cortex considered to be area 19 in New World monkeys by Brodmann[8-10]. The discoveries that area 17 and 18 each correspond to separate representations of the visual hemifield have led to the widespread expectation that area 19 also corresponds to a single representation. We have previously discussed the evidence supporting that view and suggested that the evidence is also compatible with the concept of a number of visual areas rather than one forming the outer boundary of V II in primates (see ref. 5).

Initial experiments on the organization of visual cortex of the owl monkey, begun in 1968, revealed that some recording sites just anterior to the representation of the lower visual quadrant in V II had receptive fields in the upper visual quadrant. Results from one early experiment are illustrated in Fig. 3. Such results were clearly inconsistent with the prevailing view of area 19 as coextensive with a mirror-image representation of area 18 or V II. It was only after a series of more extensive experiments that it became apparent that these receptive fields in the upper visual quadrant were part of the visual area we now term DM, and that area 19 was not a single subdivision of visual cortex as classically defined in New World monkeys, but consists of part or all of several visual areas including DL (see ref. 5), DI, DM, M (see ref. 3) and at least one additional tentorial area on the ventral surface of the occipital lobe. This series of extrastriate cortical visual areas adjoining V II in the owl monkey stands in marked contrast to the single area, V III, corresponding to area 19 in the cat[14,24].

The connections of DM

As a separate subdivision of the visual system, DM would be expected to have a distinct pattern of connections with other visual structures like those demonstrated for area 18 (see ref. 23) and the middle temporal visual area (MT)[18,21,22]. One source of input to DM appears to be from MT. Spatz and Tigges[21] showed that lesions in MT in marmosets resulted in degeneration in a number of regions of visual cortex, and one locus of degeneration (their focus 7) was in dorsomedial cortex in the position where we would expect DM to be located. In another study, Tigges *et al.*[23] made lesions in the part of area 18 on the dorsolateral surface of the occipital lobe of squirrel monkeys and found dense fiber degeneration in the region of the dorsolateral crescent (DL) with a second, sparser zone of degeneration in the region of DM. More recently, Wagor *et al.*[25] have found terminal degeneration in a number of areas of visual cortex after lesions in DM. Each part of DM projects through the corpus callosum to the comparable part of DM of the opposite cerebral hemisphere. On the same side as the lesion, DM projects to MT, DL, and the posterior parietal cortex just anterior to DM. Subcortical connections are also to visual structures, *i.e.*, the superior colliculus, the pretectum, pons, and parts of the pulvinar complex[19]. These pathways into and from DM form part of the argument that the area is a separate and distinct subdivision of the visual system.

DM as a second order transformation

A number of visual structures such as V I (ref. 2), MT (ref. 1), LGN (ref. 16), the superior colliculus[17], and the inferior pulvinar[7] form simple topological transformations of the contralateral half of the visual field. In such *first order* transformations, all adjacent points in the hemifield are represented in adjacent points in the structure. In *second order* transformations, adjacent points in the hemifield are not always represented next to each other in the structure. This second type is found in V II (ref. 4) and DL (ref. 5) where the representation of the horizontal meridian splits a few degrees out from the center of gaze, and consequently neighboring points on each side of the horizontal meridian may be represented in quite distant loci within each of the two cortical areas. As is shown in Figs. 2 and 4, DM is a second order transformation. Except for the central 15° or so, the representations of the upper and lower quadrants are separated along the horizontal meridian and displaced laterally and medially so that stimulation of some loci just above and below the horizontal meridian may activate neural populations as much as 8 mm apart.

Congruent and incongruent borders between adjacent visuotopic structures

In a *congruent* border between adjacent visuotopic structures, adjacent loci on opposite sides of the border represent very similar parts of the visual field, and there is a correspondence in the visuotopic organization of the two abutting structures so that, for example, a superior to inferior progression or a central to peripheral progression on one side of the border is matched by a similar progression on the opposite side of the border in the adjoining structure. Examples of congruent borders corresponding to the vertical meridian representation include the V I-V II border[2,11] and the MT-DL border[5]. An example of a congruent border corresponding to the horizontal meridian is the V II-DL border[1,5]. A congruent border corresponding to the temporal periphery of the lower visual quadrant is part of the DM-M border. Congruent borders

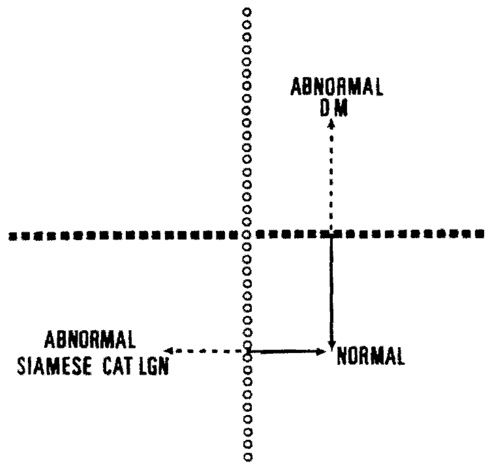

Fig. 8. Normal visuotopic organization compared with the abnormal visuotopic organization found in the lateral geniculate nucleus of Siamese cats and in the abnormal segment of DM in owl monkey 71-185. The circles indicate the vertical meridian; the solid squares indicate the horizontal meridian. The solid arrows indicate the normal direction and distance from the horizontal and vertical meridians; the dashed arrows indicate the abnormalities in visuotopic organization found in Siamese cats and in owl monkey 71–185.

in which much or all of the contralateral hemifield is represented include the borders between the laminae in the lateral geniculate nucleus[16] and the border between the lateral geniculate nucleus and the inferior pulvinar[7].

While receptive fields near the DM-V II border in both areas are located near the horizontal meridian, the DM-V II border is *incongruent* because of the mismatching of the visuotopic organizations of the two adjoining areas. This mismatching occurs because relatively peripheral receptive fields along the horizontal meridian are located at both ends of DM, while in the adjacent part of V II, the progression is from more central receptive fields laterally to more peripheral receptive fields medially (see Fig. 2). Such mismatches are of interest since they show that complete matching along the borders of adjoining areas does not always occur. It would be interesting to determine whether congruent and incongruent borders have any functional or developmental significance.

Abnormal visuotopic organization

In owl monkey 71-185, the receptive fields of neurons in the abnormal segment of DM are located approximately the normal distance from the horizontal and vertical meridians appropriate for their positions within the visuotopic map of DM, but they are located on the *wrong side of the horizontal meridian.* This abnormality is analogous to the defect present in the lateral geniculate nucleus of Siamese cats[13,15] in which the receptive fields of neurons in the abnormal segment are located approximately their normal distance from the horizontal and vertical meridians but on the *wrong side of the vertical meridian* (see Fig. 8).

The defect in the visuotopic organization of the lateral geniculate nucleus in

Siamese cats results from an abnormal projection of some of the fibers from the developing retina to the lateral geniculate on the wrong side of the brain. Specifically, some of the retinal fibers that would normally be destined to terminate in ipsilateral laminae of the lateral geniculate, actually terminate in the contralateral geniculate in a pattern mirror symmetrical about the vertical meridian to their normal visuotopic organization. We know nothing of the mechanism which produced the abnormal segment of DM in owl monkey 71-185 nor whether it was produced by a genetic mutation or some developmental anomaly. Nevertheless, the existence of the types of abnormal visuotopic organization found in Siamese cats and in this single owl monkey may provide clues to the code for laying down visuotopic organization in the developing mammalian brain. These types of abnormal visuotopic organization involving mirror symmetrical defects about the vertical and horizontal meridians suggest that the developmental code for normal visuotopic organization in mammals may include 4 essential features: (1) distance from the vertical meridian; (2) side of the vertical meridian (*i.e.*, right or left half of the visual field); (3) distance from the horizontal meridian; (4) side of the horizontal meridian (*i.e.*, upper or lower quadrant).

We have no way of knowing how commonly there occur such cases of abnormal visuotopic organization as we have found in owl monkey 71-185. We have observed no other such abnormality in any other experiment in the course of mapping other visuotopic structures in the brains of primates. However, such abnormalities may be much more common in domesticated animals that are no longer subjected to the rigors of natural selection. Abnormalities in visuotopic organization due to genetic mutations, such as the one found in Siamese cats, may arise and be perpetuated in lines of domesticated animals that would not be perpetuated from generation to generation in the wild state. Similarly, in man, who through his culture is essentially self-domesticated, such differences in neural organization may arise and be perpetuated from generation to generation, and such variants may account for some individual differences in perceptual and cognitive capacities.

ACKNOWLEDGEMENTS

The experiments reported in this study were conducted at the Department of Neurophysiology, University of Wisconsin. We thank Dr. Leon Schmidt, Southern Research Institute, Birmingham, Alabama, for providing the owl monkeys used in this study. Mr. F. M. Miezin helped in some of the data collection. Histological materials were prepared by Mrs. I. Lucey and Mrs. J. Eckleberry. Figures were drawn by Ms. D. Urban, and photographic work was by Mr. T. Stewart. Dr. Joel Myerson and Ms. Evelynn McGuinness provided useful comments on the manuscript.

Supported by NINDS Grants NS-05326, NS-06225, NS-12131; NSF Grant GB-36779; and an Alfred P. Sloan Fellowship to J.M.A.

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 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.

3 Allman, J. M., and Kaas, J. H., A visual area adjoining the second visual area (V II) on the wall of parieto-occipital cortex of the owl monkey (*Aotus trivirgatus*), *Anat. Rec.*, 178 (1974) 297–298.

4 Allman, J. M., and Kaas, J. H., The organization of the second visual area (V II) in the owl monkey: a second order transformation of the visual hemifield, *Brain Research*, 76 (1974) 247–265.

5 Allman, J. M., and Kaas, J. H., A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey (*Aotus trivirgatus*), *Brain Research*, 81 (1974) 199–213.

6 Allman, J. M., Kaas, J. H., and Miezin, F. M., A dorsomedial visual area adjoining VII in the owl monkey (*Aotus trivirgatus*), *Soc. Neurosci. Abstr.*, 1 (1971) 126.

7 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.

8 Brodmann, K., Beiträge zur histologischen Lokalisation der Grosshirnrinde, die Rindenfelder der niederen Affen, *J. Psychol. Neurol. (Lpz.)*, IV (1905) 177–226.

9 Brodmann, K., Beiträge zur histologischen Lokalisation der Grosshirnrinde: VII. Die cytoarchitektonische Cortexgliederung der Halbaffen (Lemuriden), *J. Psychol. Neurol. (Lpz.)*, 12 (1908) 287–334.

10 Brodmann, K., *Vergleichende Lokalisationslehre der Grosshirnrinde*, Barth, Leipzig, 1909, 324 pp.

11 Cowey, A., Projection of the retina onto striate and prestriate cortex in the squirrel monkey, *Saimiri sciurus*, *J. Neurophysiol.*, 27 (1964) 366–396.

12 Cragg, B. G., 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.

13 Guillery, R. W., and Kaas, J. H., A study of normal and congenitally abnormal retinogeniculate terminations in cats, *J. comp. Neurol.*, 143 (1971) 71–100.

14 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.

15 Hubel, D. H., and Wiesel, T. N., Aberrant visual projections in the Siamese cat, *J. Physiol. (Lond.)*, 218 (1971) 33–62.

16 Kaas, J. H., Guillery, R. W., and Allman, J. M., Some principles of organization in the dorsal lateral geniculate nucleus, *Brain Behav. Evol.*, 6 (1972) 253–299.

17 Lane, R. H., Allman, J. M., Kaas, J. H., and Miezin, F. M., The visuotopic organization of the superior colliculus of the owl monkey (*Aotus trivirgatus*), and the bush baby (*Galago senegalensis*), *Brain Research*, 60 (1973) 335–349.

18 Lin, C. S., Wagor, E., and Kaas, J. H., Projections from the pulvinar to the middle temporal visual area (MT) in the owl monkey (*Aotus trivirgatus*), *Brain Research*, 76 (1974) 145–149.

19 Norden, J. J., and Kaas, J. H., Some subcortical projections of the dorsomedial area (DM) of visual association cortex in the owl monkey (*Aotus trivirgatus*), *Anat. Rec.*, 181 (1975) 436.

20 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.

21 Spatz, W. B., and Tigges, J., Experimental-anatomical studies on the 'middle temporal visual area (MT)' in primates. In `Efferent corticocortical connections in the marmoset (*Callithrix jacchus*)', *J. comp. Neurol.*, 146 (1972) 451–463.

22 Spatz, W. B., and Tigges, J., Studies on the visual area MT in primates. II. Projection fibers to subcortical structures, *Brain Research*, 61 (1973) 374–387.

23 Tigges, J., Spatz, W. B., and Tigges, M., Efferent cortico-cortical fiber connections of area 18 in the squirrel monkey (*Saimiri*), *J. comp. Neurol.*, 158 (1974) 219–235.

24 Tusa, R. J., The retinotopic organization of V.1, V.2, and V.3 in the cat, *Anat. Rec.*, 181 (1975) 497.

25 Wagor, E., Lin, C. S., and Kaas, J. H., Some cortical projections of the dorsomedial visual area (DM) of association cortex in the owl monkey, (*Aotus trivirgatus*), *J. comp. Neurol.*, 163 (1975) 227–249.

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