A CRESCENT-SHAPED CORTICAL VISUAL AREA SURROUNDING THE MIDDLE TEMPORAL AREA (MT) IN THE OWL MONKEY *(AOTUS TRIVIRGATUS)*

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SUMMARY

The visuotopic organization of the cortex adjoining the middle temporal visual area (MT) of the owl monkey was determined by relating receptive field locations to microelectrode recording sites. A representation of the contralateral half of the visual field was found in a histologically distinct crescent-shaped area which wraps around MT. The representation in the crescent is not a simple transformation of the visual hemifield like the primary visual area and MT. Instead, the representation of the upper and lower quadrants of the visual field are in the separate ends of the crescent just as the upper and lower quadrants are split along the horizontal meridian and represented in opposite ends of the second visual area (V II)[5]. The posterior border or base of the crescent adjoins V II, and the visuotopic organizations of MT and the crescent together form a miniature mirror-image of the V I–V II system.

INTRODUCTION

Until recently, it has been popular to describe the cortical visual system of primates as consisting of a primary receiving area, striate cortex (area 17) or V I, two successive visual belts, areas 18 and 19 or V II and V III, and temporal visual association cortex. These concepts stem from the early histological descriptions of the visual belts by Brodmann[9] and the fortuitous discovery of the importance of the temporal lobes in vision by Schäfer[35] and by Klüver and Bucy[26]. Evidence has now accu-

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mulated that the cortical system is more complex than previously thought. This evidence has been of several types. For example, from the behavioral alterations following differently placed lesions of the temporal lobes in rhesus monkeys, Iwai and Mishkin[23] concluded that temporal visual cortex has at least two functional subdivisions. It also has become apparent that different parts of temporal and occipital cortex receive visual information from the superior colliculus via a relay in the pulvinar complex[16,19,20,27,29]. In addition, studies of cortico-cortical connections have revealed a complexity of visual projections and interconnections beyond those compatible with previous schemes of cortical organization[37,39,43,44,48,49].

The actual number, extent, and internal organization of the subdivisions of visual cortex are best revealed by the microelectrode mapping method. When critical recording sites are marked with microlesions, or in some other manner, so that mapping information can be related to cortical architecture, the method has proven to be a powerful approach for defining subdivisions of visual cortex[1,2,6,18,22,24,25,31]. The method has also been invaluable in revealing the organization of cortex responsive to auditory[30] and somatic[33] stimuli. By applying the microelectrode mapping method to visual 'association' cortex in the owl monkey, we soon realized that the visually responsive cortex was much more extensive than was previously thought, and that most of it consisted of a series of separate representations of the visual field[1,3,6,7]. Our goal became to describe these subdivisions in detail and to see if they could be identified in other primates. The first area described was the middle temporal visual area (MT)[1] in the upper temporal lobe, which we also found in the prosimian, *Galago senegalensis*[6].

In the present report, evidence is presented for considering part of the visually responsive cortex bordering MT as a distinct area. A crescent-shaped band of cortex surrounding most of MT contains a complete representation of the visual hemifield. This cortex is histologically distinct from adjacent cortex and occupies part of what would be considered area 19 in primates. Because of its location in the occipital–temporal cortex and its shape, we refer to this subdivision as the dorsolateral crescent (DL). The dorsolateral crescent is not a simple topological transformation of the visual hemifield; like the second visual area (V II), DL is split along all but the central part of the horizontal meridian, so that the horizontal meridian forms the outer boundary of the crescent.

METHODS

The experimental procedures have been described previously[1]. The visuotopic organization of the dorsolateral crescent was explored extensively with electrophysiological mapping methods in 3 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 ipsi-
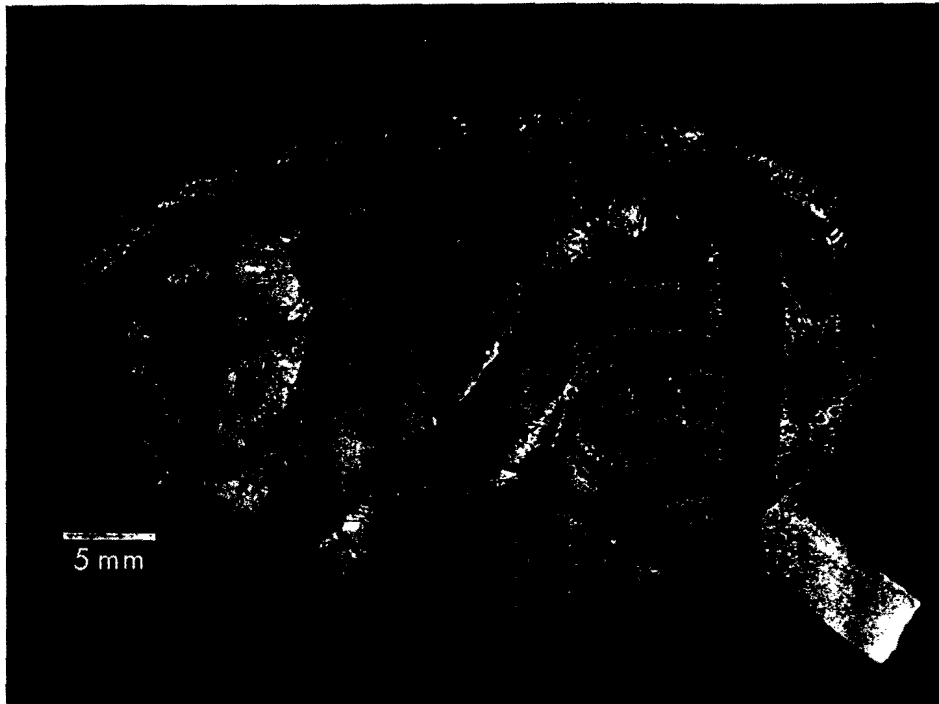
Fig. 1. The location of the dorsolateral visual area (DL) on a dorsolateral view of the left cerebral hemisphere of an owl monkey. The middle temporal visual area (MT), second visual area (V II) and the first visual area (V I) are also shown. The anterior border of cortex responsive to visual stimuli, (Visual) is marked by V's. Small circles indicate the representation of the vertical meridian, black squares denote the horizontal meridian, and the black triangle marks part of the border of the area corresponding to the margin of the temporal periphery of the visual field.

lateral eye was 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 tracts and recording sites were located in the histological sections and related to receptive fields.

RESULTS

(1) The location of DL. The location of the dorsolateral visual area on the surface of the owl monkey brain is shown in Fig. 1. The area forms a crescent around the middle temporal visual area (MT), enclosing all but the most rostral tip of MT. The lower wing of DL extends anteriorly under MT onto the posterior bank of the upper end of the middle temporal sulcus. Posteriorly, DL is bordered by the second visual area, V II (see ref. 5). Dorsally and ventrally, DL is bounded by other subdivisions of cortex that are also responsive to visual stimuli. However, the organizations of these

bordering areas have not yet been determined in detail. The wings of DL just above and below MT are in the temporal lobe, while the part between MT and V II is in a portion of the belt-like region considered by Brodmann[9] to be area 19 in New World monkeys.

(2) The visuotopic organization of DL. The organization of DL can be determined by relating the locations of receptive fields to their respective recording sites. The results from one experiment are illustrated in Fig. 2. First, it can be seen that the contralateral visual hemifield is represented in the cortex enclosed by DL (*i.e.*, MT) in the manner previously described for MT[1,6]. Receptive fields near the center of gaze are found for the most posterior recording sites in MT (sites 48–51). The peripheral parts of the visual hemifield are represented anteriorly in MT (sites 7–10, 14–19). The lower visual quadrant is in the dorsal half of MT, and the upper quadrant is in the ventral half. Within the area, any two adjacent receptive fields correspond to two adjacent recording sites. Thus, MT, like V I, is a simple topological transformation of the visual hemifield. We have referred to this type of representation as a *first order transformation*[4,5].

By comparing the receptive field locations for DL with those for MT in Fig. 2, it can be seen that DL is organized like MT in some ways. The receptive fields for recording sites 47, 55, 56, 57, and 58 indicate that central vision is represented posteriorly in DL as it is in MT. Likewise, receptive fields for recording sites 1–3, 11, and 20–22 show that the more peripheral parts of the hemifield occupy the anterior portions of DL. Finally, as in MT, the ventral half of DL represents the upper visual quadrant while the dorsal half relates to the lower visual quadrant.

In one way, however, the organization of DL is basically different from MT. The upper and lower quadrants of the visual hemifields are represented in separate wings of DL. Thus, adjacent receptive fields just above and below the horizontal meridian often relate to quite separate recording sites in DL. For example, receptive fields 1 and 22 border each other at the horizontal meridian, but the recording sites are located 5 mm apart. The receptive fields for recording sites 4 and 46 are another example of this spatial separation. The representation can be considered to be split along all but the central part of the horizontal meridian, so that the horizontal meridian both divides the area into upper and lower halves and forms most of the outer boundary. The inner boundary, shared with MT, is the vertical meridian. We have called this type of distortion of the visual hemifield a *second order transformation*[4,5].

Other examples of receptive fields for recording sites in DL are shown for a second experiment in Fig. 3. The results support the conclusions based on the first case. Receptive fields 9 and 22, for instance, are close to each other in the upper and lower quadrants respectively, while the corresponding recording sites are more than 7 mm apart. In addition, this second experiment shows more of the representation of the periphery of the lower visual quadrant (RFs 2, 3, 4) than did the first experiment. Results from other experiments are in general agreement with those illustrated in Figs. 2 and 3.

As indicated by the data illustrated in Figs. 2 and 3 and as shown in the summary
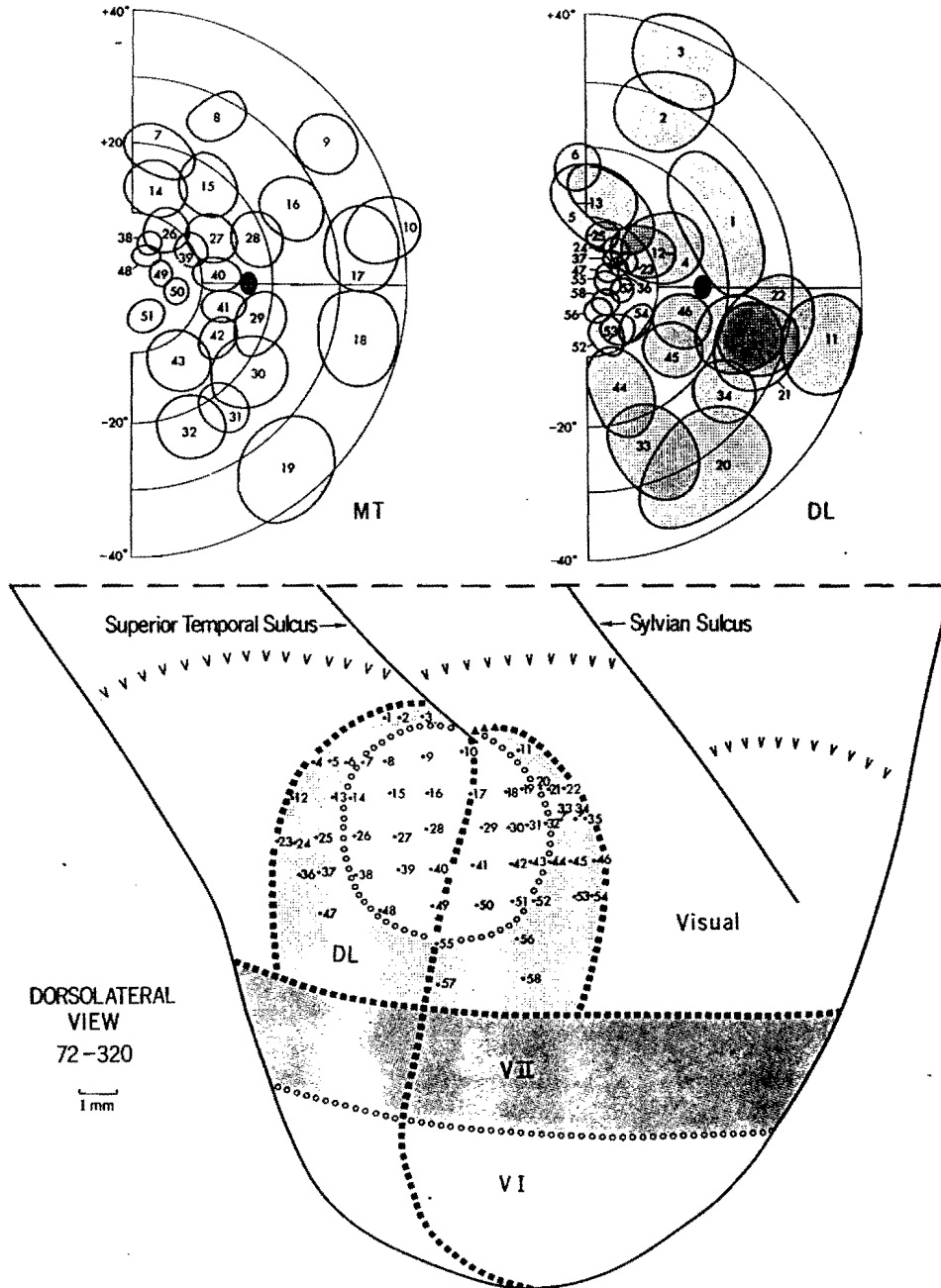
Fig. 2. Receptive fields for recording sites in DL and MT of an owl monkey. Numbered dots mark electrode penetrations on a dorsolateral view of the posterior half of the left cerebral hemisphere in the lower part the figure. Above, the corresponding receptive fields are indicated on perimeter charts of the contralateral hemifield for MT (left) and DL (right.)
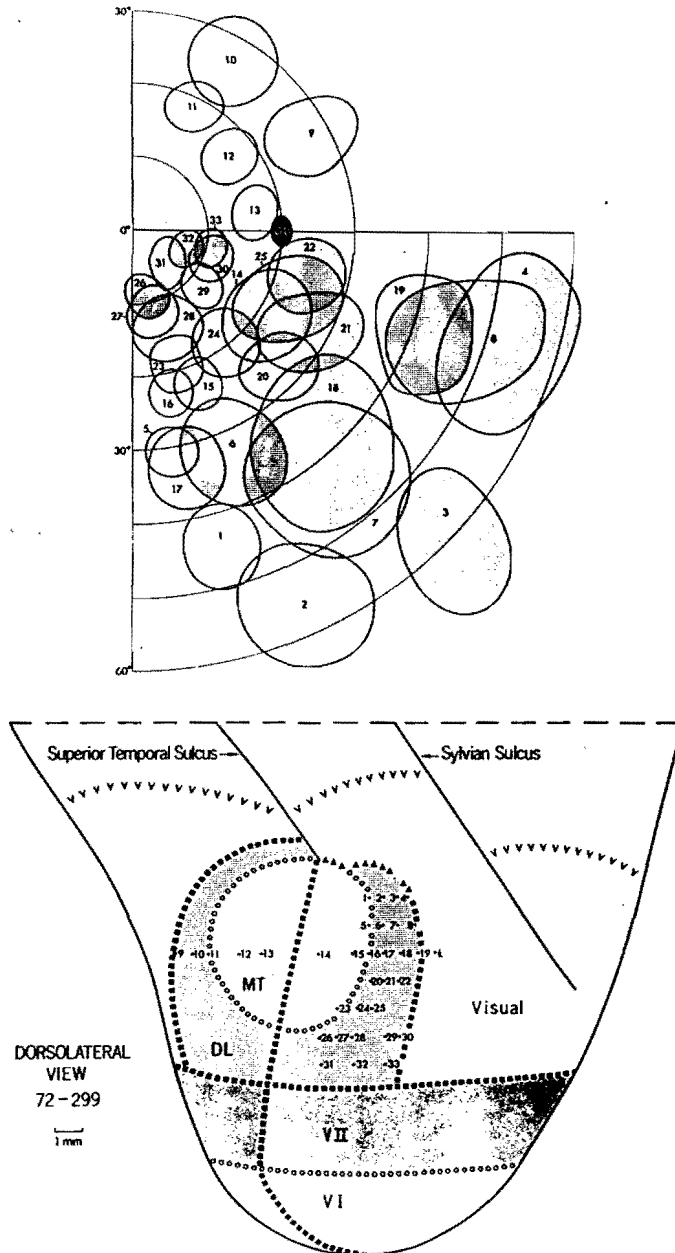
Fig. 3. Receptive fields for recording sites in DL and MT of an owl monkey. Conventions as in Fig. 2.

diagrams in Fig. 6, over half of DL is devoted to the central 10° of the visual hemifield. The relative amount of cortex devoted to the central visual field appears to be proportionally greater in the crescent than in MT[1,6], DM[7], M[3], V I[2], or V II[5].

The properties of neurons in DL were not studied in detail. Moving bars of light or shadow were effective stimuli and the borders of receptive fields were well

defined. During the course of some experiments, responses became sluggish in DL or the area became unresponsive while responses from MT or V I remained vigorous.

(3) The cortical architecture of DL. During the electrophysiological experiments, cortical recording sites judged to be at the borders of DL were often marked with small electrolytic lesions. Later, these experimental brains were processed, and sections were stained for cell bodies or for myelinated fibers. In this way it was possible to determine the architectonic characteristics of DL as a subdivision of visual cortex. The results indicate that DL can be identified from architectonic characteristics as well as by visuotopic organization. All parts of DL were found to be lightly myelinated in comparison with adjoining areas, and light myelination was the most useful feature in identifying the area. Some of the histological characteristics of DL can be seen in Figs. 4 and 5 (also see Fig. 7 of a previous report[1] where DL was labeled '19').

Sections from the brain of the experiment illustrated in Fig. 3 are shown in Figs. 4 and 5. From the electrophysiological results, recording site 16 of Fig. 3 was judged to be just outside of DL and into MT, and a microlesion was made at this recording site. In the upper brain section in Fig. 4, it can be seen that the lesion is just within the area of heavy myelination, MT. In the lower sections which were stained for cell bodies, DL is less easily distinguished from MT, but some differences are apparent. MT has a greater number of large pyramidal cells in the deeper part of layer III than does DL, and layer V and VI are somewhat more easily distinguished by differences in cell packing in MT than in DL. The recording site marked 'L' in Fig. 3 was thought to be just outside of the dorsal margin of DL and into an adjoining representation of the visual hemifield which we have tentatively termed the dorsal intermediate area (DI). The lesion at this recording site is on the right side of the brain sections in Fig. 4, marking the dorsal boundary of the lightly myelinated cortex, DL.

In the experiment illustrated in Fig. 3, a microlesion was used to mark the border of DL on the ventral side of MT. The brain sections shown in Fig. 5 indicate that the lesion is just within the densely myelinated MT. It is also apparent from the figure that the cortex in the temporal lobe just ventral to DL is more myelinated than DL. Thus, DL can be distinguished from other visual cortex in the temporal lobe, from MT, and from DI. The differences between DL and area 18 have been shown previously (see '18' and '19' in Fig. 7 of ref. 1).

DISCUSSION

The results indicate that there is a representation of the visual hemifield in the cortex surrounding most of the middle temporal visual area (MT) in the owl monkey, *Aotus trivirgatus.* The representation is histologically distinct from MT and other adjoining cortex. We have called this cortex the dorsolateral crescent (DL) because of its location and shape.

MT and DL as an analogue of the V I–V II system. A similarity in the visuotopic organization of the paired visual areas, MT and DL to a second pair, V I and V II, is apparent in Fig. 6 where these 4 areas are illustrated in a schematic unfolding of the
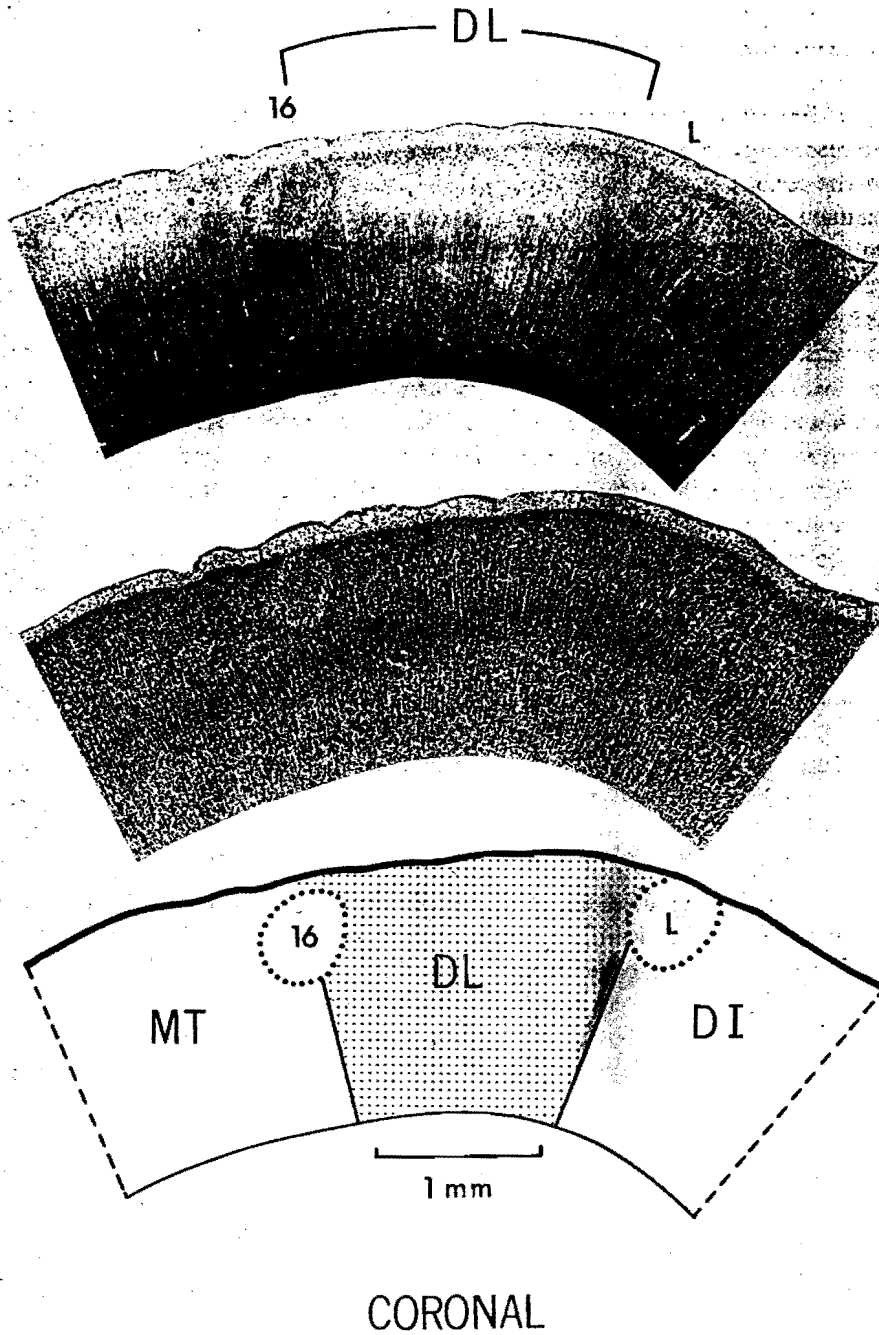
Fig. 4. Photomicrograph of the dorsal part of DL with microlesions marking boundaries as determined electrophysiologically in the experiment illustrated in Fig. 3. The lesions were at recording sites 16 and L of Fig. 3, and adjacent coronal brain sections through the lesions are stained with hematoxylin for myelin (above) and thionin for cells (middle). Note the light myelination of DL in comparison with the middle temporal visual area (MT) and the dorsal intermediate visual cortex (DI).
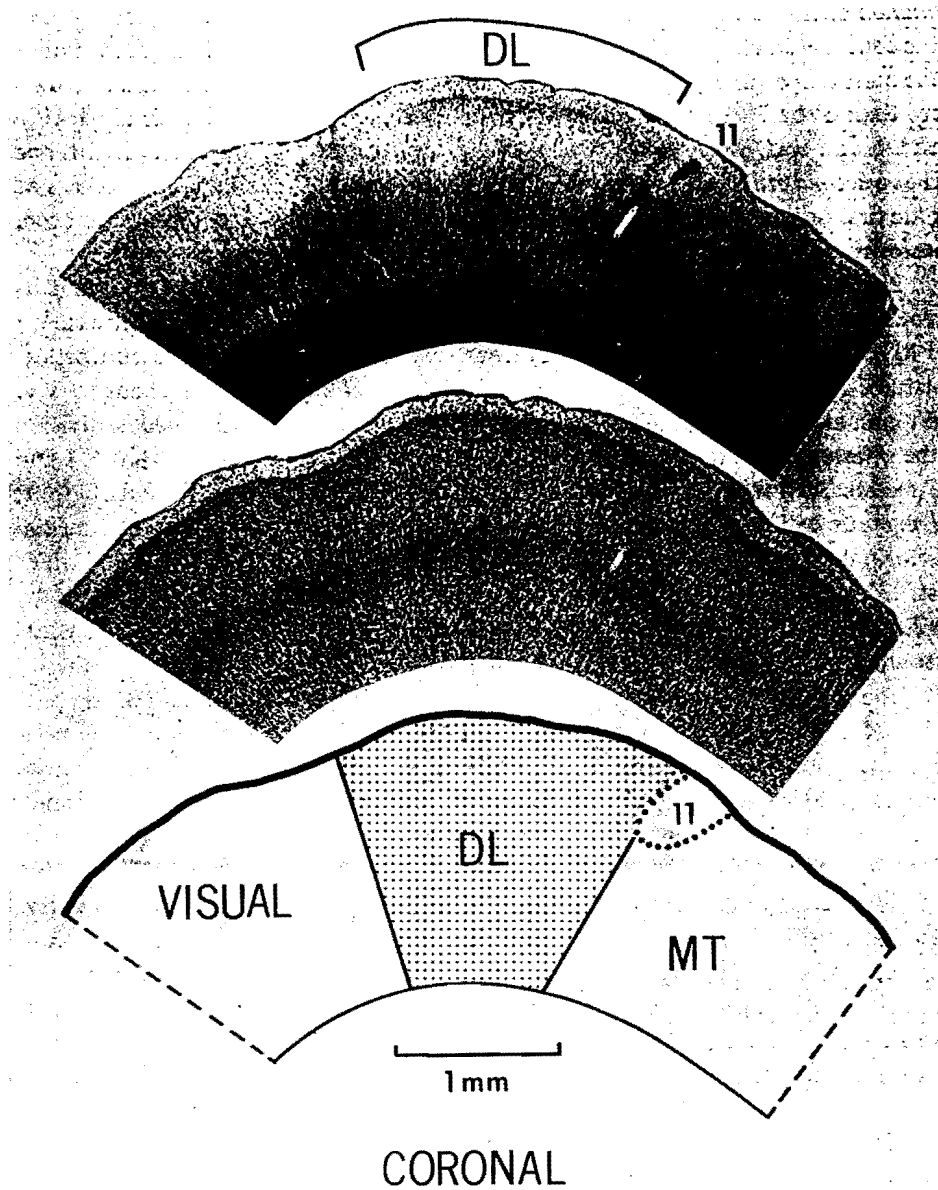
Fig. 5. Photomicrograph of the ventral part of DL with a microlesion marking the boundary with MT. The lesion was at recording site 11 of Fig. 3. Conventions as in Fig. 4. Note the light myelination of DL in comparison with MT and visual cortex of the temporal lobe (visual).

visual cortex. The topographic organization of MT and DL together is essentially a miniature mirror-image of the V I–V II system. MT, like V I, is a simple topological transformation of the contralateral half of the visual field in which all adjacent points in the hemifield are represented in adjacent points in the cortex. We have termed the type of visuotopic organization present in V I and MT a *first order trans-*

formation of the visual hemifield[4,5]. In contrast, in both DL and V II adjacent points in the contralateral half of the visual field are *not* always represented in adjacent points in the cortex. Specifically, adjacent points on opposite sides of the horizontal meridian more than 6° or 7° from the center of gaze are represented in quite distant loci in both DL and V II. We refer to the type of visuotopic organization present in DL and V II as a *second order transformation* of the visual hemifield[4,5]. Thus, both MT and V I are first order transformations almost completely surrounded by the second order transformations DL and V II respectively.

Further striking parallels exist between the V I–V II system and MT and its surrounding crescent. An important resemblance is that each of the center areas, V I and MT, receives a major and independent visual afferent input from a subcortical structure. Input from the retina is relayed in the lateral geniculate nucleus to V I. The retina also projects to the superior colliculus, which projects to a medial division of the inferior pulvinar[29], which in turn projects to MT[27]. In addition, both V I and MT feed back to the thalamic visual structures from which they receive visual input; V I projects to the lateral geniculate nucleus[10,21], while MT projects to the medial inferior pulvinar[38]. Thus, in several ways MT is like V I. Even histological similarities exist. Like V I and other primary sensory receiving areas, MT is distinguished by bands of densely myelinated fibers in brain sections stained for myelin[1,6,37], while surrounding areas, DL and V II, are less densely myelinated.

The parallel between the two cortical systems extends to the nature of the projections from the first order transformation upon the surrounding second order transformation. V I projects in a systematic fashion upon V II, and investigations in primates[36,42,44] have shown that the portion of V I devoted to the horizontal meridian more than a few degrees from the center of gaze projects to *two* loci in V II which correspond to the representations of the horizontal meridian in the nearly separate upper and lower visual quadrant representations in V II. Similarly, Spatz and Tigges[37] have shown that lesions placed in the center of MT and thus straddling the representation of the horizontal meridian result in *two* foci of degeneration immediately flanking MT on its medial and lateral aspects (see foci 2 and 4 of their Plate 1). These two flanking zones of degeneration presumably lie within DL and suggest that MT projects onto DL in a manner very similar to the projection of V I onto V II.

More recently, Tigges *et al.*[42] reported a topographic projection of V II back upon V I, thus demonstrating the existence of reciprocal connections between homotopic loci in V I and V II. This finding, together with the observation that it appears to be more important for sites in V II to be in close spatial proximity to sites in V I *than to other sites in V II*, caused us to propose that V II may be a functional adjunct of V I and that V I and V II together might be regarded as a functional unit[5]. While such reciprocal connections between DL and MT have not yet been demonstrated, the question we pose is whether MT and DL might be regarded as paired areas forming a larger functional unit of visual cortex similar to the V I–V II unit.

If the MT–DL unit evolved independently of the V I–V II unit, this would suggest that only certain ways of representing space and forming pairs of closely inter-

acting visual areas are possible or advantageous. Thus, the V I–V II unit was an adaptive structure for handling visual information, and a second such unit somehow emerged under the constraints of the primate visual system. On the other hand, the development of the MT-DL unit might have had something to do with the prior existence of a genetic code for elaborating the V I–V II unit. In a previous paper[1], we speculated on how multiple sensory representations in the cerebral cortex might have evolved. As the results of genetic mutations, whole visual areas might have been replicated in the cortex so that two practically identical areas would come to exist where previously only one had existed. In following generations, a gradual modification of one or both of the areas would occur, with a gradual divergence of structure and functions. This idea is similar to that of the paleontologist Gregory[17] who proposed that a common mechanism of evolution has been the sudden replication or duplication of body parts followed by a divergence of structure and function. A comparable view has also been developed by the geneticist Ohno[32] who stressed the role of gene duplication and redundancy in evolution. Duplicated genes escape the pressures of natural selection operating on the original gene and thereby can accumulate mutations which enable the new gene to perform previously non-existent functions. It seems possible that the V I–V II system might have become replicated, starting out as almost identical mirror images and developing distinct patterns of structure and function over
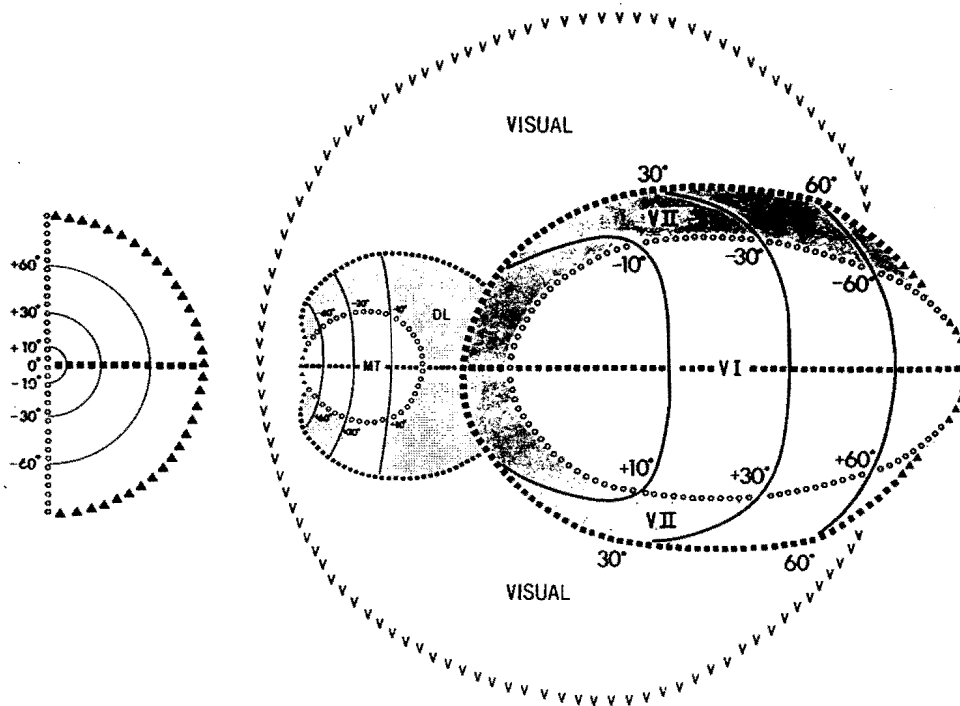

Fig. 6. A schematic representation of visual cortex in the owl monkey. V I and V II form one pair of representations of the visual field, while MT and DL form a second pair of representations as a smaller mirror image of V I and V II. Conventions as in Fig. 2.

many generations. In any case, it is intriguing that paired first and second order transformations occur at least twice in the primate visual cortex.

DL and the concept of area 19 as a third visual area (V III). Most anatomists and physiologists have adopted Brodmann's view that visual cortex in primates and most other mammals consists of 3 functional subdivisions — areas 17, 18, and 19. Talbot and Marshall[41] and Talbot[40] presented early electrophysiological evidence that areas 17 and 18 were each representations of the visual hemifield, *i.e.*, V I and V II respectively. Further studies on a number of species, demonstrating both the architectonic distinctiveness of areas 17 and 18[2,5,9,11,18,22,24,25] and the details of the visuotopic maps that are coextensive with these areas[2,5,12,14,18,22,24,25,31,40,41,45,47] leave little doubt about the validity of these conclusions for V I and V II. However, the evidence is less convincing that a single architectonic subdivision, area 19 or V III, forms the complete outer boundary of area 18 or V II. Furthermore, the concept is in conflict with the evidence that for some primates area 18 is bordered by a number of visual areas, including DL (see below).

The term V III was introduced by Hubel and Wiesel[22] after they used micro-electrodes to explore part of the cortex designated as area 19 in the cat. A third representation of part of the visual field was found, leading to the conclusion that a third representation of the visual hemifield is coextensive with area 19. The concept of area 19 as V III in the cat was supported by the anatomical studies of Hubel and Wiesel[22], later reports of the connections of the visual areas[15,46], and summary diagrams and statements of other electrophysiological investigations[8,45,46]. However, the organization of only a limited portion of area 19 was established, and the evidence was compatible with both the idea of area 19 as V III and the idea of a zone bordering area 18 which consists of a number of distinct visual areas. Recently, a more extensive electrophysiological exploration of area 19 in the cat has been undertaken (Tusa, personal communication), and it appears that the hypothesis of area 19 as V III as proposed by Hubel and Wiesel[22] is basically correct for the cat.

As in the cat, electrophysiological evidence has indicated an additional visual area adjoining V II in the squirrel[18]. This evidence was used to argue for a single area, V III, occupying a single architectonic zone, area 19, adjoining the outer border of area 18. Similarly, our own previously published[1] receptive fields for recording sites in DL between MT and V II were first seen as evidence for V III since the results were consistent with the concept of a single bordering area. However, as with the early electrophysiological evidence in the cat, the results from both the squirrel and the owl monkey were also compatible with the concept of V II being bordered by several visual areas. In New World monkeys, area 19 has been described as a narrow band of cortex bordering the outer margin of area 18 (see ref. 9) including the zone between area 18 and the cortex now identified as MT[1,6]. As so defined, area 19 includes that part of DL representing central vision and most or all of several other visual areas[3,7] (unpublished findings). These more extensive electrophysiological results have caused us to abandon the concept of area 19 as a third systematic representation of the visual field in the owl monkey.

The patterns of projections from V I and V II have been used to argue for V III

in monkeys[13,48,49]. However, the disclosed projections have been from only a limited part of these first two visual areas and only indicate the existence of a visual area bordering part of V II. Recently, Tigges *et al.*[43] presented the issue in their report of the projections of area 18 in the squirrel monkey. The projections from area 18 indicated the presence of a topographically organized representation in 'area 19'. The lesions were in parts of area 18 on the dorsolateral surface, and the zones of degeneration were in a limited part of area 19 on the dorsolateral surface. The authors pointed out that such results do not conflict with either Brodmann's[9] classical concept of area 19 or with an alternative concept of a series of discrete bordering areas; however, they note that a determination of the projections of those portions of area 18 that represent the peripheral visual field (on the medial wall and in the calcarine fissure) should yield results that support only one of these two views.

The pattern of projections from MT to the surrounding cortex in the marmoset[37] strongly suggests the existence of DL in this New World monkey, and it is reasonable to assume that DL is a feature common to all New World monkeys. We have previously demonstrated the presence of MT in the prosimian *Galago*[6], and the preliminary data suggest the existence of DL in this primate. The presence of MT and the possible existence of DL in the *Galago* suggest that these areas emerged early in evolution before the divergence of monkeys and prosimians. Evidence has been accumulating for MT in Old World monkeys[48,50], and it would be surprising if the MT–DL unit is not present in all existing primates.

It is possible that a single visual area, V III, borders V II in some mammals such as the cat, whereas primates and perhaps other mammals are more complexly organized, with a number of visual areas bordering V II. Recent evidence suggests that even in rabbits[47] and rats[31], several extrastriate areas may border V II, and it is not yet certain how many visual areas adjoin V II in other mammals. Thus, it remains an intriguing possibility that this number varies from species to species and in different lines of descent and that an increase in the number of visual areas in evolution led to development of new behavioral capacities related to vision.

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