Short Communications

The dorsal third tier area in *Galago senegalensis*

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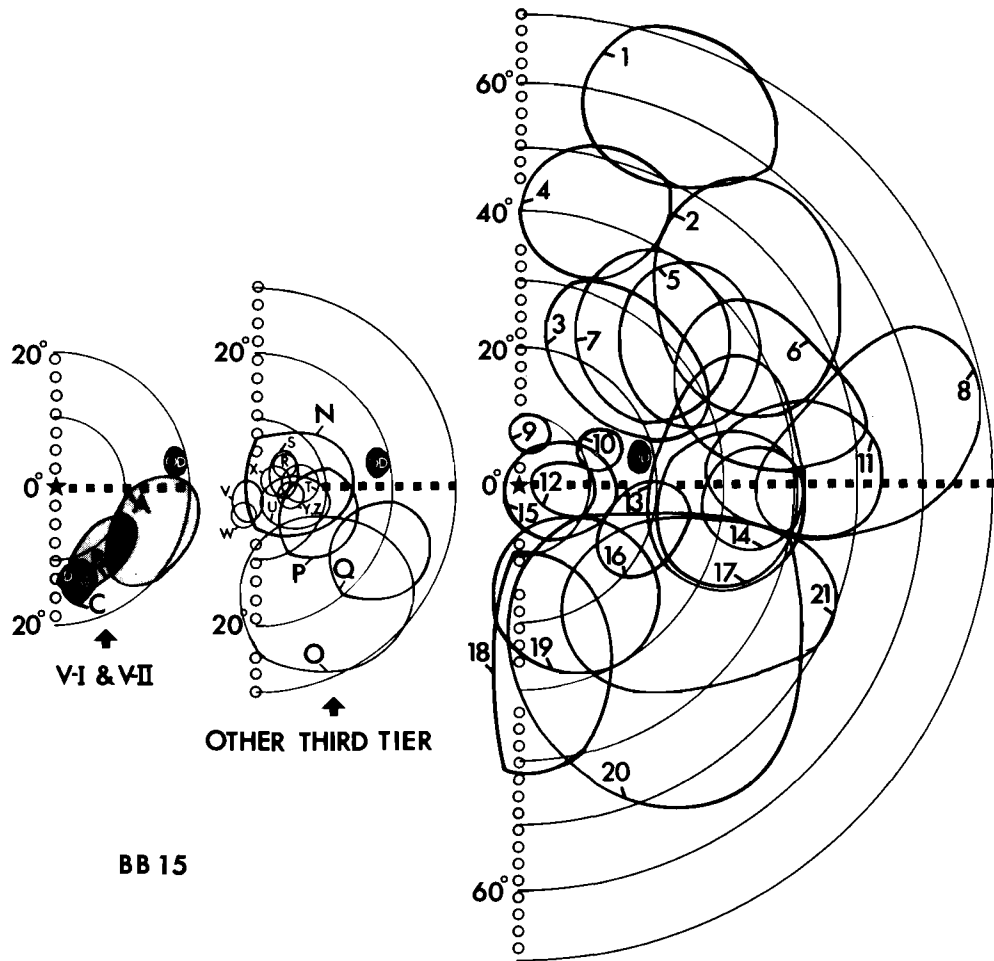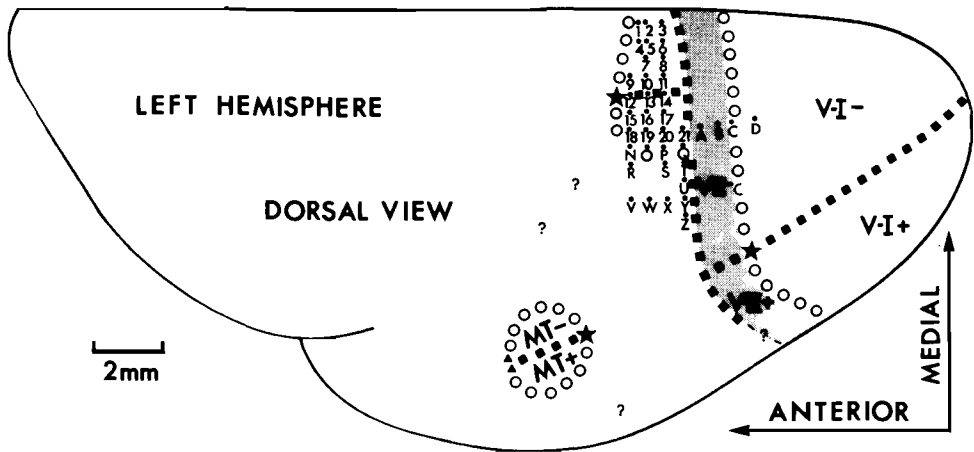
Five extrastriate visual field representations adjoin the anterior border of V-II in the owl monkey and collectively comprise a third tier of visual areas in this species[1,5-7,10]. We have sought to determine whether the presence of a third tier of visual areas is a characteristic feature of visual cortex organization in primates. The order primates contains two suborders: the haplorhines (tarsiers, monkeys, apes and man) and the strepsirhines (lorisoids and lemuroids)[8]. We have found in a strepsirhine species, *Galago senegalensis*, that there exists a third tier of visual areas, one of which, the dorsal area, is described in detail in this paper. This finding together with recent evidence from haplorhine species suggests that a third tier of visual areas is a characteristic feature of visual cortex organization in primates[1,13].

The receptive field organization of the dorsal third tier area and adjacent cortex was mapped by recording from single neurons and small clusters of neurons with microelectrodes in 161 penetrations in 4 galagos. In order to make more efficient use of our experimental primates, we have developed a chronic technique for recording repeatedly from the visual cortex in animals that have been tranquilized. By using this technique, the animal can be used in many experimental sessions and returned to its cage in good condition after each session.

Each galago was prepared for chronic recording by attaching a stainless steel recording chamber to the skull with Grip dental cement under general anesthesia (Ketamine 40 mg/kg) and aseptic conditions. The chamber overlies a craniotomy giving access to visual cortex. At the beginning of each experimental session, the galago was tranquilized with a single injection of triflupromazine (20 mg/kg) and loosely wrapped in a towel. The galago's head was restrained with a circular clamp attached to a cylindrical adapter that was screwed onto the implanted chamber. The cornea, sclera and eyelids on the side contralateral to the chamber were topically anesthetized with 0.5% dibucaine in contact lens wetting solution. The eyelids were retracted with tape. An eye ring, which was machined to fit the contour of the eye, was

60°

40°

20°

0°

20°

V-I & V-II

N

P Q

O

OTHER THIRD TIER

BB 15

-1

4

-2

-5

3 -7

6-

8

-9

-10

11

12

13

15

14

16

17

21

18 -19

20

60°

LEFT HEMISPHERE

DORSAL VIEW

2mm

V-I -

V-I +

MT -

MT +

MEDIAL

ANTERIOR

cemented to the right eye with a fast-acting tissue adhesive, histoacryl blue (Tri Hawk International, Montreal, Canada). The eye ring was mounted on a stem attached to a ball joint that could be moved or locked in place. The cornea was protected from drying with a contact lens of zero power. An additional spectacle lens was used when necessary to focus the retinal image on a plastic hemisphere (30 cm radius) centered on the right eye. The inner surface of the hemisphere was sandblasted to provide a ground surface screen. The image of the retinal blood vessels was projected onto the hemisphere by means of light originating from a fiber optic source placed near the eye and reflected from the tapetum onto the hemisphere[11]. These images were traced on the hemisphere with a china marker. In order to avoid retinal bleaching and discomfort to the galago, the level of illumination from the fiber optic was kept dim. The room lights were turned off during this procedure, and the experimenter dark-adapted prior to tracing the images of the retinal vessels on the hemisphere.

The implanted recording chamber was filled with sterilized mineral oil warmed to 37 °C. The chamber was then sealed to reduce brain pulsation, but the interior of the chamber remained clearly visible through the lucite cover plate. The microelectrode was positioned with a specially designed device that rotated on the cylindrical adapter screwed to the chamber and could be locked in any desired position. A sterilized microelectrode enclosed in an electrically shielded holder was advanced hydraulically approximately perpendicular to the surface of the dorsal area. Glass insulated platinum-iridium microelectrodes[14] were used to penetrate the dura and record the activity of single neurons or small clusters of neurons, which was amplified and led to an audio monitor. Receptive fields were mapped with light slits and dark bars projected on the surface of the hemisphere. Immediately after mapping each receptive field, the fiber optic light source was switched on and the position of the retinal blood vessels was determined. It was thus possible to monitor eye position precisely throughout the course of the experimental session.

The brains of 2 galagos were sectioned at 40 μm and stained with cresyl violet for

Fig. 1. Receptive field organization of the dorsal area in the galago. The 3 perimeter charts illustrate portions of the right hemifield of the right eye and contain receptive fields A, B, C and D recorded from V-II and V-I, fields N–Z recorded from another third tier area and fields 1–21 recorded from the dorsal area. The black ovals marked OD indicate the projection of the optic disk in the visual field. The small circles indicate the vertical meridian (midline) of the visual field; the small black squares lie on the horizontal meridian. The star located at the intersection of the vertical and horizontal meridians indicates the center of gaze which is the projection of the retinal area centralis[9]. The lower diagram is a dorsal view of the left cerebral hemisphere of BB 15. Recording sites 1–21 are located in the dorsal area. The black squares, the circles and the star indicate the representations of the horizontal meridian, vertical meridian and center of gaze. The location of the border between V-I and V-II and the middle temporal area (MT) border are based on a reconstruction of cell and myelin-stained histological sections from BB 15. The projection of the visual field in V-I, V-II and MT are based on other electrophysiological mapping experiments[4,9]. V-I+, V-II+ and MT+ contain representations of portions of the right upper quadrant; V-I—, V-II— and MT— contain representations of portions of the right lower quadrant. The small black triangles on the anterior border of MT indicate the representation of the extreme temporal periphery of the contralateral hemifield. The size of MT in this individual galago is smaller than that found in a previous investigation in this species[4].

cell bodies and hematoxylin for myelin. Unlike the middle temporal area[2,4,12] or the dorsomedial area of the owl monkey, the dorsal area does not appear in sections stained with these techniques to be histologically distinctive from surrounding cortex. Two of the galagos in which the dorsal area was mapped are being used in a quantitative investigation of the response properties of single neurons by S. Petersen and J. Allman.

The dorsal area was mapped in 62 penetrations in 4 galagos. The organization of the dorsal area shown in Fig. 1 is based on the locations of receptive fields for 21 penetrations within the area for one animal (BB 15). The dorsal area was mapped in comparable detail and with very similar results in a second galago. The dorsal area has also been mapped with similar results in 2 other galagos, which are the subjects of ongoing studies of the properties of single neurons. In the lower part of Fig. 1, there is a dorsal view of the left hemisphere showing the surface locations of the micro-electrode penetrations for the numbered recording sites. In the upper right part of Fig. 1, the positions of the corresponding receptive fields are indicated on the large perimeter chart. The medial and slightly greater half of the dorsal area contains the upper quadrant representation; the lateral and lesser half of the area contains the lower quadrant representation.

The anterior border corresponds to the vertical meridian (midline) representation. We were unable to obtain visual responses in the region immediately anterior to the dorsal area in BB 15, but in 21 penetrations in 2 other galagos we recorded neurons with large ill-defined visual receptive fields in this region, which may correspond to posterior parietal cortex in owl monkeys[1,2].

The most peripheral lower quadrant receptive fields were recorded from the lateral margin of the area. Lateral to the dorsal area lie recording sites N–Z. We believe these sites are located in another third tier visual area since their receptive fields are much more central than the receptive fields for adjacent sites 18, 20 and 21 in the dorsal area. The receptive fields recorded from this region are generally much smaller than those recorded from the representation of the central visual area in the dorsal area. We have explored the region between the dorsal area and the middle temporal area (MT) in 37 penetrations in 3 galagos, and this region, which emphasizes the central portion of the visual field, contains a visual area that appears to correspond to the dorsolateral area (DL) in the owl monkey[4,5]. The reversal in receptive field organization at the border between the dorsal area and the more lateral third tier area, illustrated in Fig. 1, was also clearly present in the other 2 galagos in which this region was explored.

The posterior and medial border of the dorsal area adjoins V-II and corresponds to the horizontal meridian. The portion of V-II adjacent to the dorsal area was mapped in 41 penetrations in 4 galagos, all of which yielded a similar pattern of visuotopic organization. The receptive fields in the progression D, C, B, A (Fig. 1) proceed from the vertical meridian near the V-I–V-II border to horizontal meridian near the V-II–dorsal area border. A similar progression is illustrated in Fig. 2, which shows the receptive fields recorded in penetration 3 of BB 15 as the microelectrode proceeded down the medial wall passing from the dorsal area into V-II. Receptive
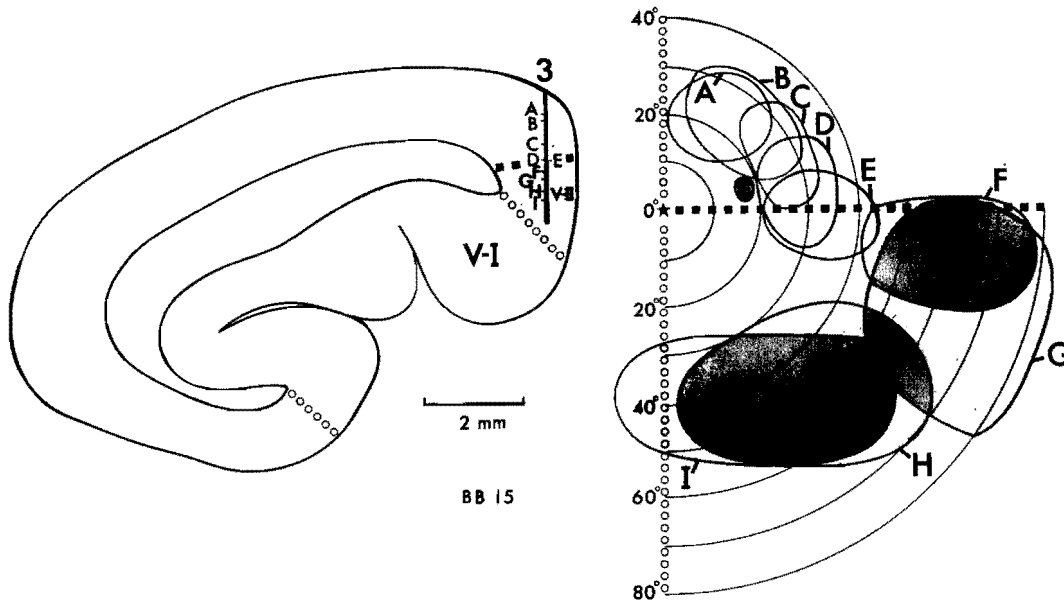
Fig. 2. Receptive field shift at the incongruent border between the dorsal area and V-II. The perimeter chart illustrates portions of the right visual hemifield and contains receptive fields A–E recorded from the dorsal area and F–I recorded from V-II. On the left is a coronal section containing microelectrode penetration 3. The small circles indicate the histological border between V-I and V-II, which corresponds to part of the vertical meridian representation on the basis of other electrophysiological experiments[9]. V-II and its receptive fields are shaded. The border between V-II and the dorsal area is shown by the black squares and corresponds to the representation of part of the horizontal meridian.

fields A–E were recorded from the dorsal area and progress toward the horizontal meridian. Receptive field F, which lies just within V-II, is located much more peripherally on the horizontal meridian. Receptive fields G, H and I progress toward the vertical meridian as the V-I border is approached.

In an earlier paper[6], the concept of congruent and incongruent borders between visual representations was advanced. In a congruent border between adjacent visuo-topic structures, adjacent loci on opposite sides of the border represent very similar parts of the visual field. Examples of congruent borders include V-I–V-II border and the MT–DL border, both of which correspond to the vertical meridian[3,5]. A certain degree of incongruence occurs at several places along the border between V-II and the third tier areas which correspond to the horizontal meridian. One of the rare examples of an abrupt shift in receptive fields at an incongruent border is illustrated in Fig. 2 where a receptive field shift of more than 25° along the horizontal meridian occurred between immediately adjacent points in the dorsal area and V-II. In a previous paper[6], evidence was presented that visuotopic organization is established in the developing cortex on the basis of two rectilinear coordinates measured in distance from the vertical and horizontal meridians (midlines). The existence of incongruent borders, near which one coordinate is largely preserved while the other is considerably distorted, is consistent with this notion. The splitting of the horizontal meridian

representation to form most of the external border of second order transformations (V-II and third tier areas) may facilitate the ontogenetic development of orderly transitions between cortical areas by insuring that at least one of the two visuotopic coordinates is held reasonably constant for much of the border.

The existence in galagos of the dorsal area which adjoins only a small portion of the anterior border of V-II indicates the presence of a third tier of visual areas in strepsirhine primates. Recent results from Old World monkeys strongly suggest that more than one extrastriate area adjoins V-II in these primates as well[13]. Thus the presence of a third tier appears to be a phylogenetically ancient feature of visual cortical organization in primates and a feature common to all primates.

It is possible that the dorsal area is a phylogenetically independent development in Galago or in strepsirhine primates; it is also possible that further investigation will provide strong evidence that it corresponds to a particular area found in other species. At present the best candidate for such a correspondence is the medial area found in New World monkeys[7]. Like the medial area, the dorsal area adjoins along the horizontal meridian the portion of V-II in which the lower field far periphery is represented. The upper and lower quadrant representations are in the same relative positions in the dorsal area as in the medial area, and in the dorsal area, as in the medial area, the more peripheral portions of the visual field are relatively better represented than in other cortical visual areas. Another area that might correspond to the dorsal area of the galago is the dorso-intermediate area of the owl monkey[1]. The upper and lower quadrant representations are in the same relative positions in both areas, and both areas adjoin the dorsolateral area. Studies now under way of the functional properties of single neurons and the anatomical connections of these areas should help to determine whether they, in fact, do correspond to one another.

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