A REPRESENTATION OF THE VISUAL FIELD IN THE CAUDAL THIRD OF THE MIDDLE TEMPORAL GYRUS OF THE OWL MONKEY *(AOTUS TRIVIRGATUS)*

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INTRODUCTION

It has long been postulated that the cerebral cortex of mammals is made up of discrete areas each of which performs a definite set of functions. Traditionally, visual cortex has been regarded as consisting of 3 architectonically distinct subdivisions, areas 17, 18, and 19, first described by Brodmann[8]. While many questions remain concerning areas 17, 18, and 19[25,29,58], the traditional view of only 3 visual areas has been modified by evidence from several different mammals that cortex rostral and lateral to areas 17, 18, and 19 also is activated by visual stimuli[4,13,18,23-25,27,35,36,49,55,57]. In the cat, at least one portion of the additional responsive region appears to systematically represent the visual field[27]. In support of the electrophysiological reports, fiber degeneration studies have revealed that striate cortex projects to cortex rostral or lateral to area 19 in squirrel monkey[47], rhesus monkey[15,59], cat[20,26,50] and opossum[3]. These reports suggest that, in addition to areas 17, 18, and 19, there may be other visuotopically organized areas in the neocortex of mammals.

If each topographical representation of the visual field has functional significance, then definition of the extent, boundaries, connections, and internal organization of each representation is basic to a total understanding of central visual mechanisms. A general theory of the functions of visual cortex also depends on establishing both the similarities and differences in the organization of the visual cortex of various mammalian species and determining the significance of these similarities and differences. From consideration of a range of distantly related species, a general understanding of the organization of visual cortex in mammals may emerge.

With this long-term goal in mind, we used microelectrode mapping techniques in combination with architectonic methods to subdivide visual cortex in a New World monkey, *Aotus trivirgatus*. Being nocturnal, the owl monkey is not a typical New World monkey. However, this species was useful since its relatively smooth cortex facilitated mapping and its large relatively immobile eye was easily fixed in place. We found an extensive zone of caudal neocortex to be responsive to visual stimuli and

evidence will be presented here for considering a small portion of this total region as a distinct visual area which has not been described previously. Descriptions of other subdivisions of visual cortex will follow in subsequent reports.

A brief abstract of the present findings has been presented elsewhere[1].

METHODS

The topography of the representations of the visual field in occipital and extraoccipital cortex was determined by relating the positions of receptive fields for single neurons or small clusters of neurons to the locations of the corresponding recording sites in 33 adult owl monkeys (*Aotus trivirgatus*) provided by the National Center for Primate Biology, Davis, Calif. Most of the results presented here are from 7 experiments in which the visuotopic organization of the posterior third of the middle temporal gyrus was explored. The methods are similar to those described in previous reports[25,29,34,39].

Animal preparation. In each experiment the animal was first anesthetized by intraperitoneal injection of a 25% urethane solution (125 mg/100 g body wt.). Supplementary doses were given as needed. The pupil of one eye was dilated with a drop of cyclogyl (cyclopentolate hydrochloride, Schieffein and Co., New York, N.Y.) and silicone fluid (dimethylpolysiloxane, Dow Corning Corp., Midland, Mich.) was spread over the surface of the cornea to prevent desiccation and clouding. A rectal thermal sensor controlled a heating pad which maintained the animal's temperature at 37°C. The trachea was cannulated and the animal was placed in a modified

Fig. 1. The owl monkey eye prepared for stimulation. The eyelids are removed and the pupil dilated. Silicone fluid (dimethylpolysiloxane) spread over the surface of the cornea prevents desiccation and clouding. The eye is immobilized by cementing a ring mounted on the apparatus to the sclera with a powerful, fast-acting physiological adhesive (alpha cyanoacrylate).

Baltimore stereotactic apparatus. The scalp was removed, the temporal and occipital muscles were reflected, portions of the parietal bone overlying the visual cortex of both hemispheres were removed with a dental drill, and the dura was reflected. A dam of acrylic plastic was formed around the opening in the skull and filled with warm mineral oil. The eyelids of one eye were removed and the eye was immobilized (Fig. 1) by cementing a ring mounted on the apparatus to the sclera with a powerful, fast-acting physiological adhesive (alpha cyanoacrylate, Toagosei Chemical Industry Co., Tokyo, Japan; Wm. A Klinger and Son, Manufacturer's Representative, 826 E. Sylvan Avenue, Milwaukee, Wisc. 53217); the eyelids of the other eye were sutured shut and covered with an opaque shield.

Recording. Recordings of extracellular potentials of single neurons and small clusters of neurons were made with tungsten microelectrodes placed in a shielded

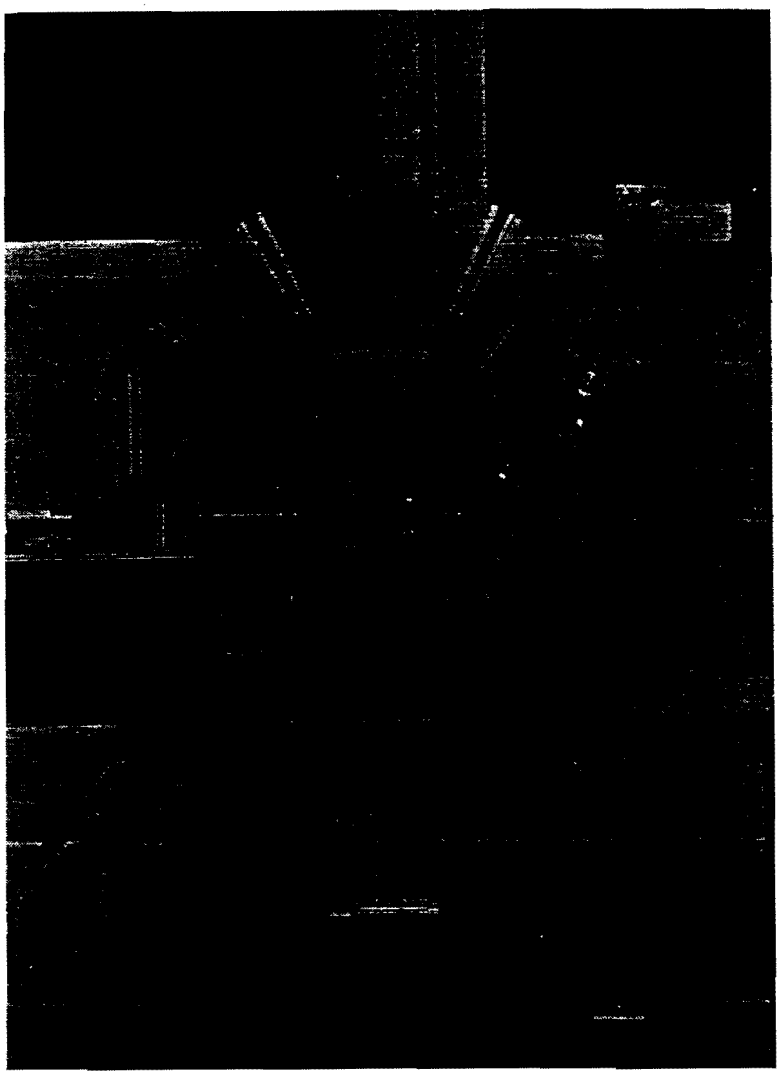

Fig. 2. A double exposure photograph of the owl monkey in the experimental apparatus. The plastic hemisphere is translucent and not transparent as it appears in the photograph.

holder and attached to a micromanipulator. The indifferent electrode was fixed to a screw in the skull. The neural activity was amplified, viewed on an oscilloscope, and heard from a loudspeaker. Responses were recorded on a Magnecord 1028 tape recorder and photographed with a Grass kymograph camera.

The site of each microelectrode penetration was marked on an enlarged photograph of the exposed cerebral cortex with the aid of a dissecting microscope. The depths of recording sites from the cortical surface were monitored on a Starrett gauge. After recording, the brains were processed for histology so that electrode tracks could be identified and related to cortical architectonics. The identification of electrode tracks was aided by marking some recording sites with electrolytic microlesions made by the passage of direct current (cathodal, 20 μA for 5 sec) through the recording electrode.

Stimuli. Small bars of light or shadow were presented on a translucent plastic hemisphere (60 cm diameter) used as the visual field of one eye. During recording, this hemisphere was placed before the owl monkey so that the immobilized eye was centered within the hemisphere (Fig. 2).

Receptive field boundaries were indicated directly on the plastic hemisphere with a wax marking pencil and were defined as the margins of the area in which visual stimuli produced an increase in the activity of the recorded neurons. The usual stimulus was a rectangular bar of light 5° long and 0.5° wide projected on the surface of the plastic hemisphere in a dimly lit room and repeatedly moved through the visual field from different angles. The boundaries of the most receptive fields were checked by using small moving shadows produced by backlighting small targets as stimuli. In order to determine the latency of the neural response, a spot of light, 3° in diameter, positioned in the receptive field of the neuron, was illuminated for 100 msec periods. The light source was a glow modulator tube (Sylvania R1131 C) similar to that used by Montero and Brugge[38]. Under the control of a Tektronix waveform generator, a vacuum tube (type 6BL7) applied a gated voltage to the glow modulator tube. A quiescent current of less than 1 μA flowing through the glow modulator tube during the 'off' phase insured the immediate ionization of gases at the beginning of the 'on' phase. Under these conditions the rise and fall times for the illumination of the glow modulator tube were found to be about 20 μsec.

Standardization of data. Data from each experiment were related to a reference zero vertical and a zero horizontal meridian through the estimated center of gaze or point of fixation. The center of gaze was not identified directly from retinal landmarks, since the owl monkey does not have a fovea[17,19,28,51] and the precise center of area centralis was difficult to locate ophthalmoscopically. Instead, the vertical meridian was established by estimating the position in the visual field of the line of decussation of the retina from receptive field positions for recording sites along the margin of striate cortex of one or both occipital lobes. The horizontal meridian was estimated from the position of the blind spot in the visual field. From retinal ganglion cell counts, Jones[28] found the center of area centralis was on the same horizontal plane as the optic disc. Therefore the horizontal meridian was defined as the line perpendicular to the vertical meridian passing through the projection of the optic disc.

Histology. At the termination of each experiment, the animal was killed with sodium pentobarbital, and the brain was removed from the skull and immersed in 10% formol–saline. A series of photographs was taken of the brain at standard views and the microelectrode penetration sites were plotted on these photographs. The brain subsequently was dehydrated, imbedded in celloidin, and sectioned at 30 μm. Alternate sections were stained with thionin for cell bodies and hematoxylin for myelin.

RESULTS

Extent of visual cortex

In 33 experiments, the posterior two-thirds of the cerebral cortex of owl monkeys was explored with microelectrodes. Neurons activated by visual stimuli were found in striate cortex and in cortex rostral to striate cortex on the dorsal surface, tentorial surface, medial wall, and both banks of the calcarine fissure. The extent of the responsive cortex on the dorsal surface is shown in Fig. 3. This responsive zone extends well beyond visual areas 17, 18, and 19 and includes large parts of extraoccipital areas 21 and 7 of Brodmann. Only the upper temporal lobe was explored and no ventral limit of responsive cortex was established for the temporal lobe. However, a rostral limit to visual cortex was established on the superior temporal gyrus in the region marked A in Fig. 3, where neurons did not respond to visual stimuli but were activated by auditory stimuli. A rostral limit to the responsive zone was also found more medially in parietal cortex between the sylvian fissure and the midline. This limit was caudal to the region responsive to somatic sensory stimuli ('So', Fig. 3). Neurons throughout this extensive region responded to stimuli within restricted areas of the visual field, although the size of the receptive fields for neurons in different cortical locations varied considerably. With each change in the locus of the cortical recording site, a change was observed in the position of the activating receptive field. Receptive field locations did not change for successively deeper recording sites within electrode penetrations perpendicular to any particular cortical surface.

It is possible to subdivide this extensive responsive region into separate areas both by differences in cortical architectonics and in patterns of visuotopic organization. In the present paper, one area, consisting of a complete representation of the contralateral visual hemifield and with distinct architectonic boundaries, is considered. This area occupies the posterior third of the middle temporal gyrus of the owl monkey and, because of its location, is termed the middle temporal visual area (MT) in this paper. The extent and location of MT are shown in Figs. 4, 5, and 6. Area MT is located just rostral to area 19 (see Fig. 6) with the major portion lying within the caudal third of the middle temporal gyrus. MT extends around the medial tip of the superior temporal sulcus onto a contiguous portion of the superior temporal gyrus. The area is oval in shape on the cortical surface with its major axis extending approximately 6 mm rostrocaudally and its minor axis about 4–5 mm mediolaterally. The estimated surface area of MT for each hemisphere is approximately 20 sq. mm compared with 260 sq. mm for striate cortex.

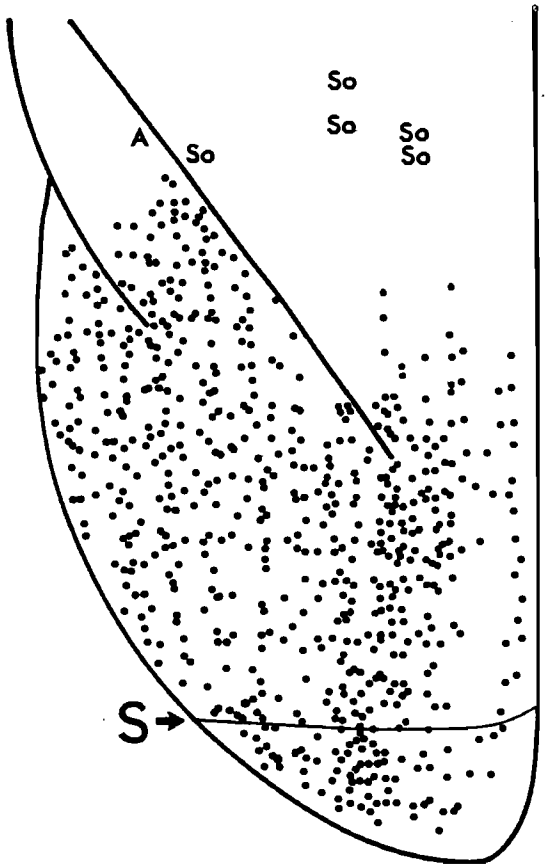

Fig. 3. Dorsal view of the caudal two-thirds of the left hemisphere of the owl monkey illustrating the distribution of visual responses in the striate and extrastriate visual cortex. Each dot indicates a recording site in the cortex for which a well-defined visual receptive field was mapped. This figure contains 638 visual recording sites from 33 experiments. Recording sites in the right hemisphere were plotted as their mirror image points in the left hemisphere. The line marked 'S' indicates the rostral border of striate cortex. 'So' indicates recording sites from which responses were evoked by somatic sensory stimulation. 'A' indicates a recording site from which auditory responses were obtained. The long fissure separating auditory and somatic cortex is the sylvian sulcus. The smaller fissure lateral to the sylvian sulcus is the superior temporal sulcus.

Architectonics of MT

The most distinguishing feature of MT is its heavy myelination, which can be readily identified even in sections of the unstained brain by the whiteness of the myelin. In brain sections stained with hematoxylin, the densely stained myelin of the deeper layers of cortex distinguishes MT from surrounding cortex and is apparent in coronal (Fig. 4), sagittal (Fig. 6) and horizontal (Fig. 7) sections. In adjacent sections stained with thionin, MT is distinguished from adjoining cortex by less dense cell packing in cortical layers IV and VI.

Area MT is not architectonically uniform in all regions, as is best seen in sagittal sections (Fig. 6). The rostral aspect of the area which extends onto the caudal wall of the superior temporal sulcus is less thick and less myelinated; cortical cells there are

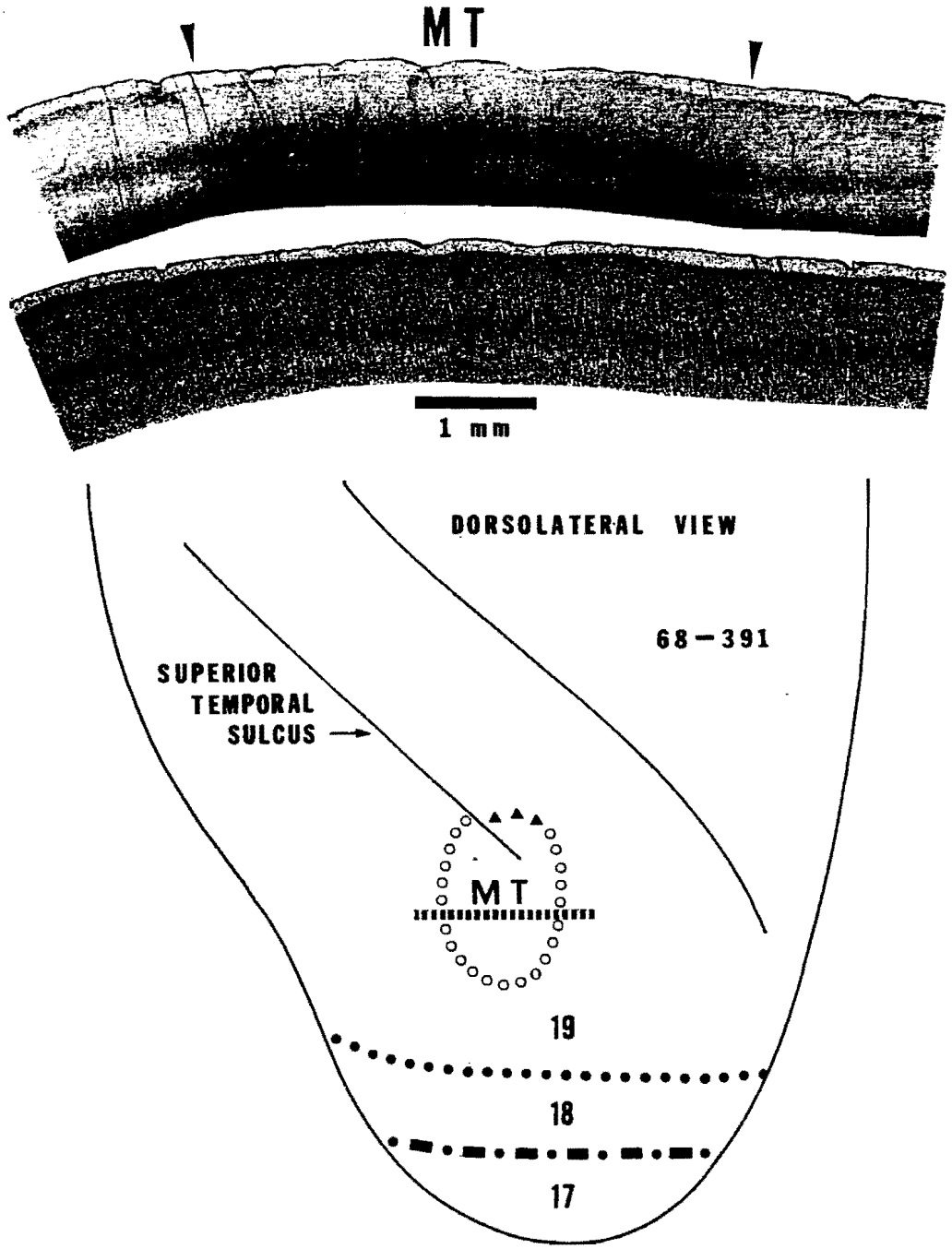

Fig. 4. Top, Photomicrographs of two adjacent coronal sections through the middle temporal visual area (MT). The upper photomicrograph was taken of a section stained with hematoxylin for myelin. The lower photomicrograph was taken of the adjacent coronal section stained with thionin. Bottom, Diagram of a dorsolateral view of the caudal half of the left hemisphere. In this diagram, the dashed line through MT indicates the level and mediolateral extent of the sections illustrated in the two photomicrographs.

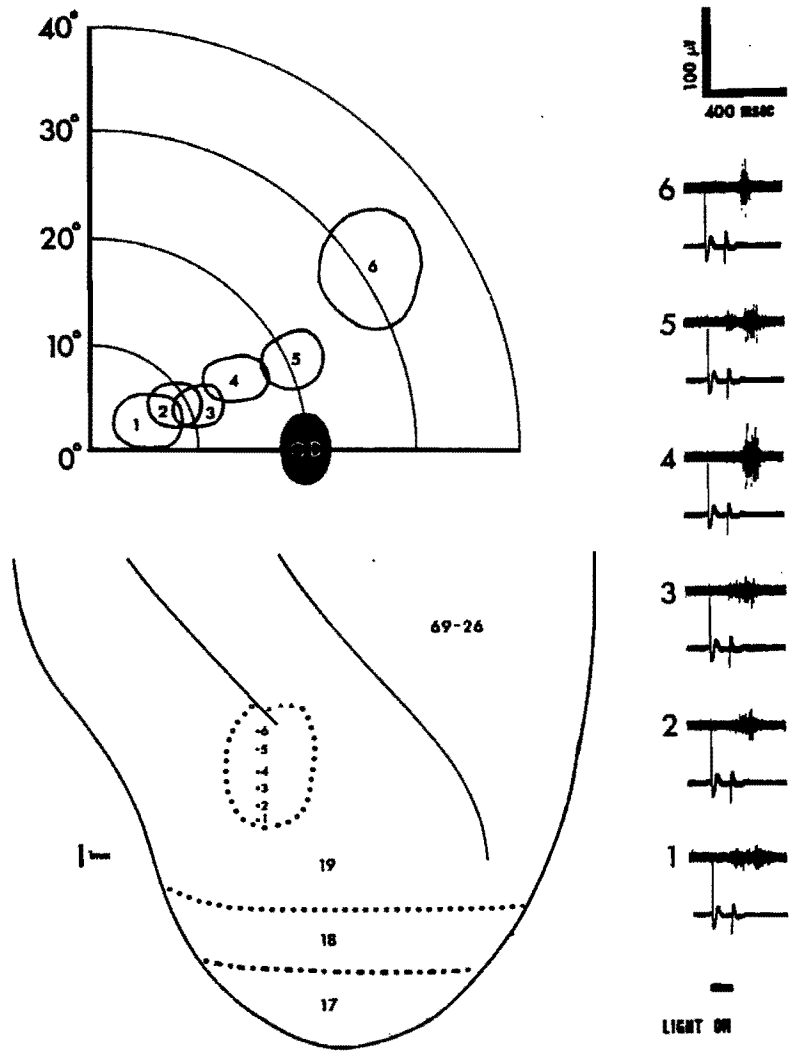

Fig. 5. Receptive fields and multiple unit responses for a row of recording sites in the middle temporal visual area (MT). The upper diagram is a perimeter chart of the central 40° of the superior temporal quadrant of the visual field of the right eye. The lower diagram is a dorsolateral view of the caudal half of the left cerebral hemisphere. On the right the upper channel of each of the 6 pairs of oscillographs 1–6 depict evoked neural activity; the lower channel contains markers for the onset and offset of illumination. In each oscillographic recording, a spot of light 3° in diameter, positioned in the receptive fields 1–6, was illuminated for a 100 msec period. The latencies of the responses were about 80 msec or longer.

more sparsely distributed. Electrophysiological results indicate that this less-developed portion of MT corresponds to the representation of the temporal periphery of the visual field (see below).

Representation of the visual field in MT

A systematic representation of the visual field in MT is revealed by orderly shifts in the locations of receptive fields corresponding to rows of recording sites

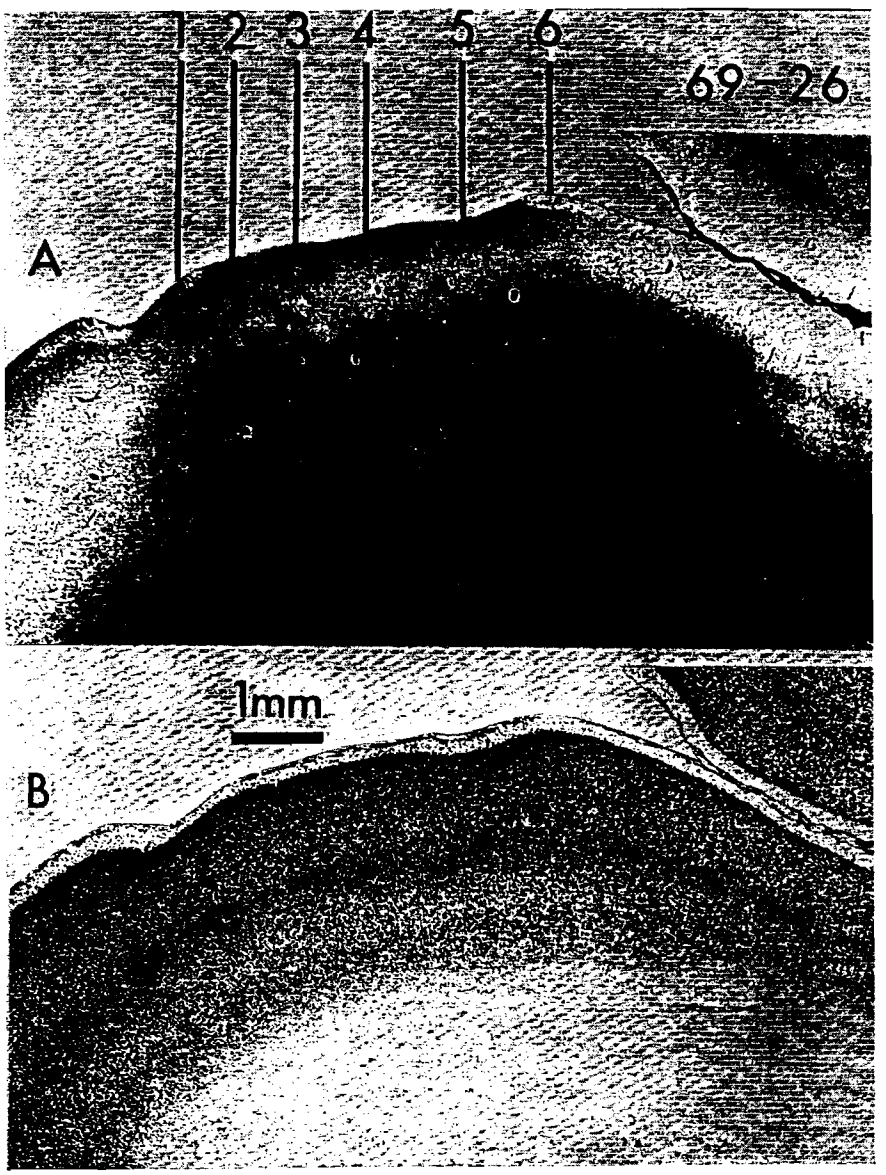

Fig. 6. Photomicrographs of adjacent parasagittal sections stained with hematoxylin (A) and thionin (B). The sections pass through the approximate plane of the recording sites for the row of receptive fields 1–6 in Fig. 5.

across the area. For example, the 6 electrode penetrations illustrated in Fig. 5 start at the caudal margin of MT and progress rostrally across approximately five-eighths of the area's length. The corresponding receptive fields begin near the intersection of the horizontal and vertical meridians and progress to about 30° in the upper quadrant of the visual field toward the temporal periphery.

A similar row of recording sites across MT is shown in Fig. 8. Again the corresponding receptive fields progress from the vertical meridian toward the periphery of the upper quadrant of the visual field. Two receptive fields were determined for two successively deeper recording sites in penetration 15 in Fig. 8. Because of the dorsal

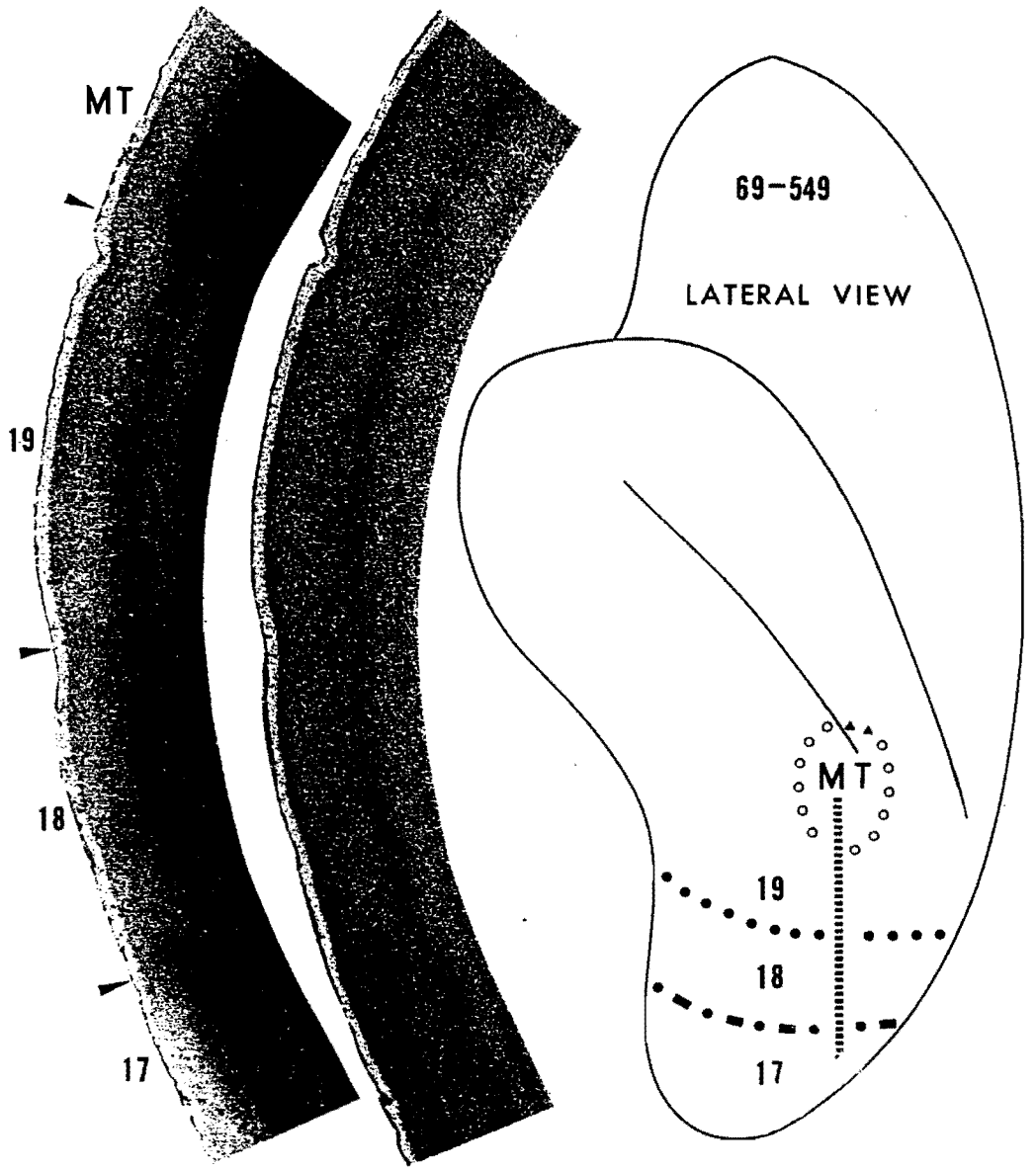

Fig. 7. Photomicrographs of adjacent horizontal sections through areas 17, 18, 19 and MT stained with hematoxylin for myelin (left) or with thionin (right). The dashed line on a lateral view of the left cerebral hemisphere indicates the rostrocaudal extent of the photomicrographs.

approach of the electrode along the wall of the sulcus, the deeper recording site is closer to the ventrolateral margin of MT and the receptive field is more peripheral and closer to the vertical meridian. In addition, receptive fields are shown for recording sites in areas 18 and 19 to illustrate that the visuotopic organization of MT is not a continuation of the organization seen in areas 18 and 19.

A more complete exploration of MT is shown in Fig. 9 with 3 caudal-rostral rows of recording sites. Again for each row, there is an orderly shift in receptive field locations, which indicates that the central and paracentral visual field is represented

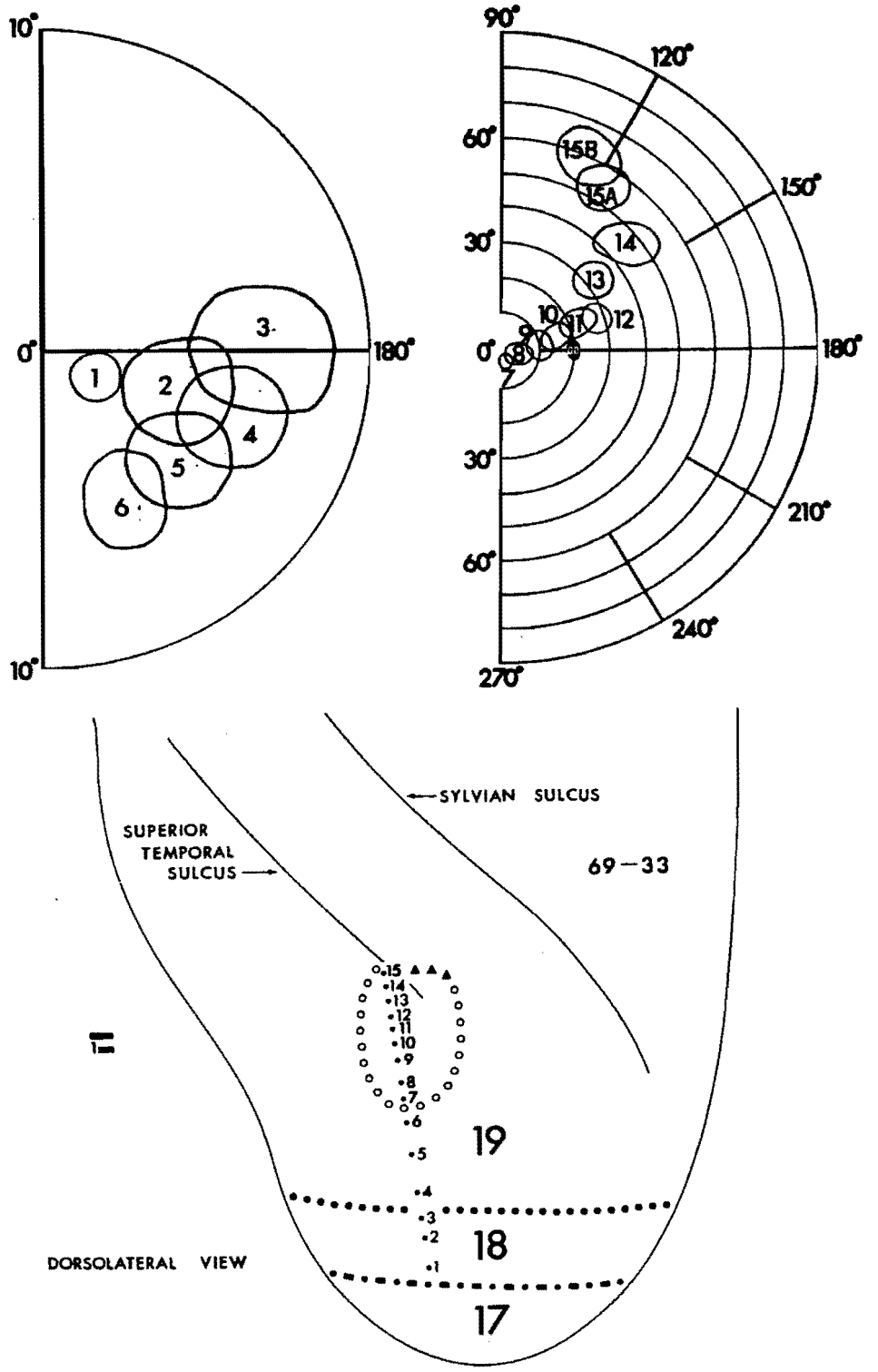

Fig. 8. Receptive fields for a row of points through areas 18, 19 and MT. The perimeter chart in the upper right corner represents the central 10° of the temporal half of the visual field of the right eye. The perimeter chart in the upper left corner represents the whole temporal half of the visual field of the right eye. Penetration 15 advanced down the caudal bank of the superior temporal sulcus. Receptive field 15A was determined for neurons 1.2 mm from the beginning of the penetration and 15B was for neurons 1.8 mm deep.

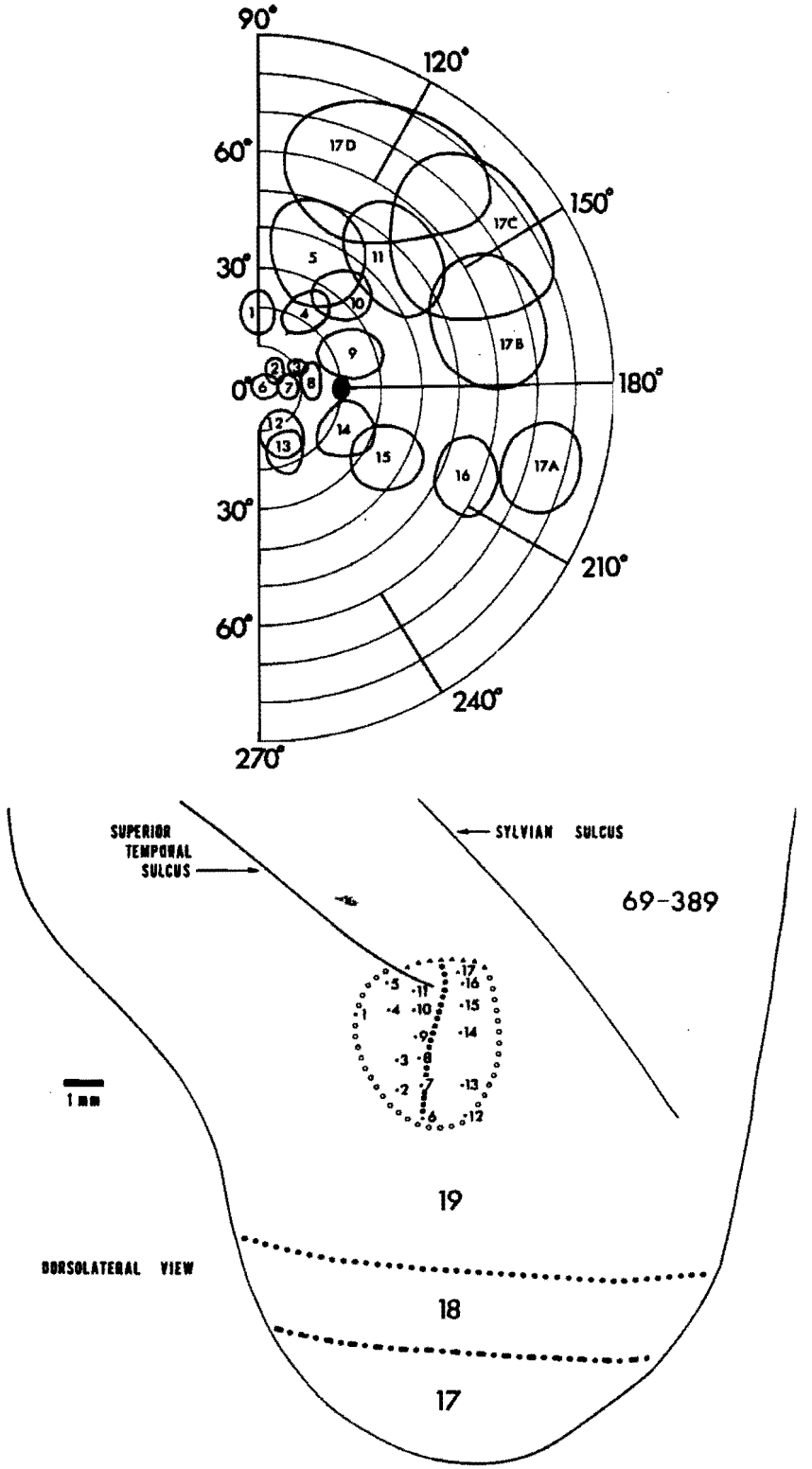

Fig. 9. The relationship of receptive field locations to recording sites in the middle temporal area (MT) in experiment 69–389. The upper diagram is a perimeter chart of the temporal half of the visual field of the right eye. The lower diagram is a dorsolateral view of the caudal half of the left cerebrum. The line of circles marks the portion of the MT border devoted to the vertical meridian and the line of black triangles indicates the portion of the MT border devoted to the temporal periphery not buried in the sulcus. The representation of the horizontal meridian, indicated by the dashed line, divides MT into a lateral portion in which the upper quadrant is represented and a medial portion in which the lower quadrant is represented. The representation of the center of gaze lies in the caudal portion of MT adjacent to area 19 and the temporal periphery is represented in the cortex around the tip of the superior temporal sulcus. In penetration 17, the electrode advanced through the cortex lying medial and slightly rostral to the tip of the superior temporal sulcus. Receptive field 17A was recorded 0.9 mm from the beginning of the penetration, 17B at 2.2 mm, 17C at 2.6 mm and 17D at 3.4 mm.

caudally in MT and more peripheral sectors of the visual field are represented rostrally. The results also show that the lower visual field is represented medially and the upper visual field is represented laterally. Thus, receptive fields 12–17A corresponding to the most medial row of recording sites (penetrations 12–17) were in the lower quadrant of the visual field; receptive fields of the middle row (penetrations 6–11) were near the horizontal meridian and slightly into the upper visual quadrant; and those of the most lateral and ventral row (penetrations 2–5) started just above the horizontal meridian and proceeded into the upper quadrant. The receptive field for neurons in penetration 1, the most lateral recording site, is consistent with the pattern of the other receptive fields and is in the upper quadrant on the vertical meridian.

The representation of the temporal periphery of the visual field is revealed by the 4 receptive fields determined for neurons at 4 successively deeper recording sites along the banks of the sulcus in penetration 17. With such a dorsal-ventral electrode penetration near the tip of the superior temporal sulcus it is possible to progress across much of the width of the rostral tip of MT. In this portion of MT, a vertical electrode penetration is oblique to the cortical surface and progressively deeper recording sites move from the lower visual field representation near the surface of the superior

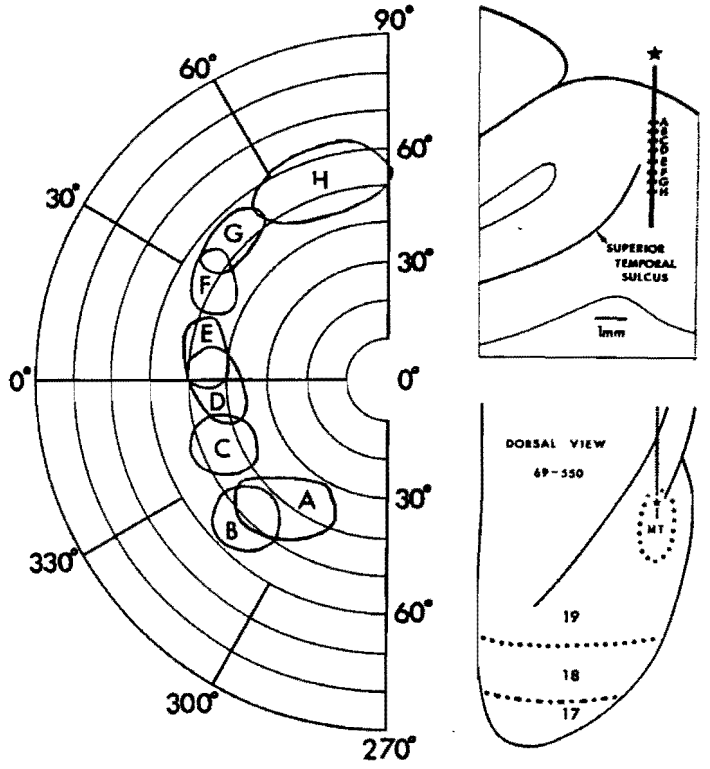

Fig. 10. Receptive fields for recording sites near the buried caudomedial tip of the superior temporal sulcus. The perimeter chart represents the nasal half of the visual field of the right eye. The diagram in the lower right corner is a dorsal view of the caudal half of the right cerebrum of the owl monkey. A star marks the location of the electrode penetration. The heavy dashed line through the star indicates the level and extent of the portion the parasagittal section shown in the upper right corner of the figure. The recording sites are identified by horizontal bars across the electrode tract.

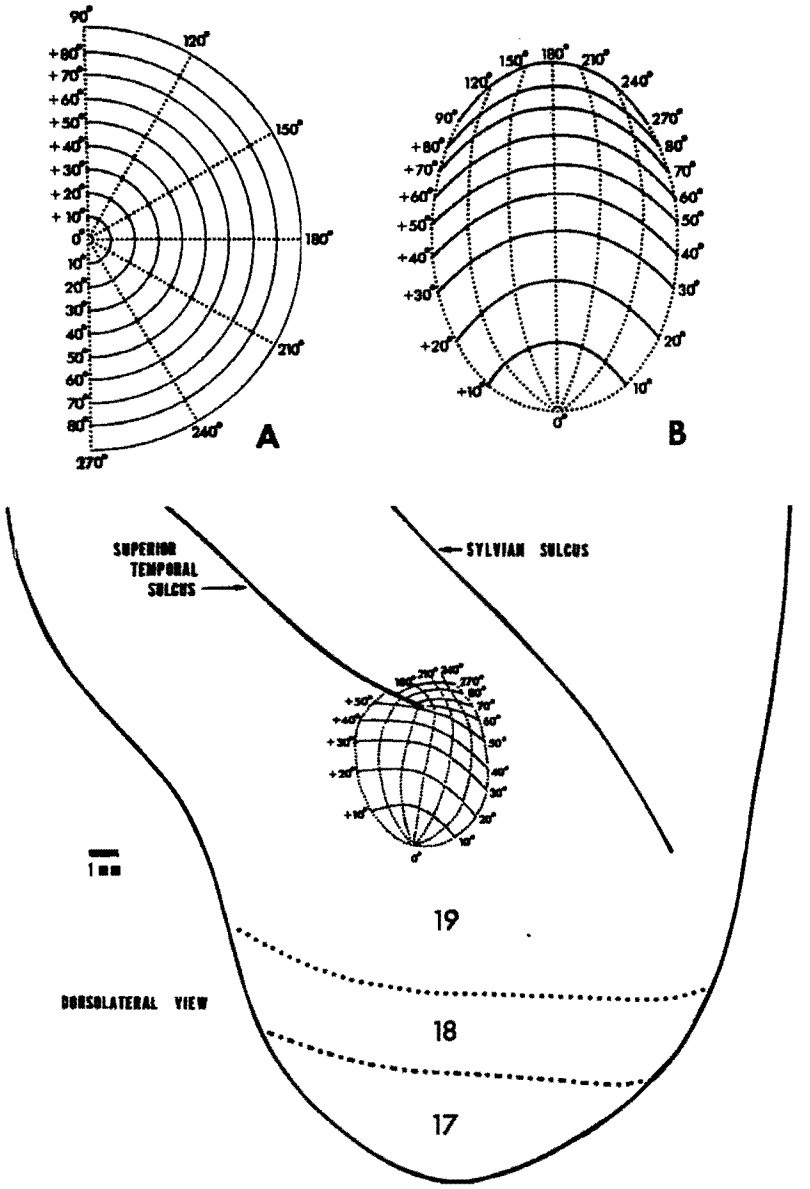

Fig. 11. The representation of the visual field on the middle temporal visual area (MT) of the owl monkey. Diagram A is a perimeter chart which is a planar representation of the contralateral half of the visual field. Diagram B is an attempt to illustrate the unfolded area MT, which is essentially an ellipse. In the lower half of the figure is a dorsolateral view of the caudal half of the left cerebrum. The coordinates of the contralateral half of the visual field have been superimposed on the cortical area, MT, as a convenient means of illustrating the pattern of visuotopic organization in MT.

temporal gyrus into the upper field representation near the buried tip of the superior temporal sulcus and finally onto the depths of the adjacent middle temporal gyrus. Thus, stimuli in receptive field 17A (in the periphery of the lower visual quadrant) activated neurons near the surface of the superior temporal gyrus while receptive fields 17B, 17C, and 17D (in the upper visual quadrant) corresponded to progressively deeper recording sites along the bank of the superior temporal sulcus and onto the

middle temporal gyrus. The representation of the periphery of the visual field in MT is further illustrated by a single electrode penetration in Fig. 10. As in penetration 17 of Fig. 9, the most dorsal recording sites relate to receptive fields in the temporal periphery of the lower quadrant of the visual field. With more ventral recording sites, the receptive fields progress systematically to 60° in the upper quadrant of the visual field. These results lead to the conclusion that the representation of the temporal periphery of the visual field is wrapped around the buried tip of the superior temporal sulcus with the lower visual field represented dorsal to the upper visual field.

The results from other experiments were consistent with those illustrated in Figs. 5, 8, 9 and 10 and the combined data were used to construct the summary diagram shown in Fig. 11. The middle temporal area, unfolded from the tip of the superior temporal sulcus, is essentially elliptical in shape with most of the border of the area representing the vertical meridian of the visual field and only a small portion representing the extreme temporal periphery. The figure illustrates the distortion of the visual field in MT caused by the disproportionately large representation of central vision.

Responses in MT

The neural activity recorded in MT was mainly from small clusters of neurons and no systematic effort was made to relate response characteristics to stimulus variables. Responses for a row of 6 recording sites in MT are shown in Fig. 5. The stimulus for these recordings was a flash of a 3° spot of light centered within the receptive field of each recording site, but a more effective stimulus at each locus was a bar of light moving through the receptive field. Although the amplitude of the responses was low, they were suitable for determining receptive field locations. As can be seen in Fig. 5, a flash of light sometimes produces both 'on' and 'off' responses. In some recording sites, only the 'off' response was observed.

DISCUSSION

Extraoccipital visual cortex

In our studies on the owl monkey, an extensive region of cerebral neocortex was found to be responsive to visual stimuli, including extraoccipital regions in the parietal and temporal lobes. Receptive fields were determined for neurons throughout the responsive zone shown in Fig. 3 and the position of the receptive field varied with the location of the electrode penetration. One subdivision (MT) of the large extraoccipital responsive region is here reported in detail and evidence has been presented that it is a complete topographical representation of the visual hemifield within a sharply delineated architectonic field. In addition, studies on macaque monkeys[23,24,33,37] suggest that portions of the temporal lobe of the owl monkey, ventral to the region we explored, also may have visual functions. Thus, the traditional view of visual cortex as consisting of only areas 17, 18 and 19 requires considerable modification and the

possibility exists that there are other distinct extraoccipital representations of the visual field in primates.

To the extent that it proves possible to subdivide the expansive extraoccipital responsive zone in the owl monkey into separate representations of the visual field, we do not think it useful to consider it is a single region under some term such as 'association cortex'. Of course, much of the responsive zone may be affected by input from nonvisual modalities, but this appears to be the case even for striate cortex[31,41,48]. It seems reasonable to presume that each systematic representation of the visual field is predominately visual in function and that each representation performs a distinct set of functions even if we do not know what those functions are.

In addition to visual cortex, the full extent of the dorsal thalamus of primates that can properly be considered visual is not completely established. Much of the pulvinar complex is implicated, since extrastriate lesions in cortex comparable to parts of the total visual region in owl monkeys are followed by retrograde degeneration of pulvinar neurons in other primates[9,12,46]. Recently, we have found a topographical representation of the visual field in the inferior pulvinar of the owl monkey[2]. From a consideration of the visual cortex and dorsal thalamus of the owl monkey, it appears that we are only beginning to understand the complexity of the primate visual system in terms of identifying the subdivisions, the internal organization of the subdivisions, and the interconnections of the subdivisions.

Evolution of multiple sensory representations

The present results add to other evidence that much of the neocortex of advanced mammals is characterized by multiple representations of sensory surfaces[16,25-27,32,43,52,53,56]. It is not clear how these multiple representations evolved. However, it appears that a common mechanism of evolution is the replication of body parts due to genetic mutation in a single generation which is then followed in subsequent generations by the gradual divergence of structure and functions of the duplicated parts[21,22]. The replication of sensory representations in the central nervous system may have followed a similar course. This possibility is an alternative to the view that topographically organized sensory representations gradually differentiated from 'unorganized' cortex or that individual topographically organized areas gradually differentiated into additional topographical representations.

Identification of MT in other species

The owl monkey is the only nocturnal New World monkey[40] and it is possible that MT is a specialization peculiar to the owl monkey. We do not favor that possibility since there is evidence for a visual area in the position of MT in two other New World monkeys, the marmoset and the squirrel monkey. In the marmoset, a region of cortex in the expected position of MT responds to photic stimuli[55]. This cortex, near the junction of the parietal and temporal lobes, borders area 19 of Brodmann[8] or area OA of Peden and von Bonin[44]. A cytoarchitectonic area closely comparable in posi-

tion and extent to MT was not identified in either Brodmann's[8] or Peden and von Bonin's[44] studies of the marmoset although the dorsal part of Brodmann's area 21 and most of Peden and von Bonin's area PFG approximate the expected location and size of MT. Perhaps both architectonic investigations identified MT but included other sectors of cortex, but not the same additional cortex, in a subdivision which contains MT. In the squirrel monkey, Spatz *et al.*[47] have recently demonstrated a projection from striate cortex to the caudal bank of the superior temporal sulcus in the expected position of MT. These investigators were not able to demonstrate a topographical organization of terminations from striate cortex, probably because the lesions in striate cortex were limited to the dorsal surface and this cortex represents only a few degrees of central vision[14]. The visual responses recorded at the dorsal margin of the superior temporal gyrus of the squirrel monkey by Doty *et al.*[18] may indicate the rostral limit to MT in that animal, but, more likely, the evoked activity was in a visual area rostral to MT, since in the owl monkey, cortex rostral to MT also is activated by visual stimuli (see Fig. 3). Although a topographical representation of the visual field has not been demonstrated in the temporal cortex of the marmoset or squirrel monkey, it seems reasonable to assume the presence of MT in these and probably other New World monkeys.

Experimental evidence also suggests the possibility of MT in the macaque monkey. A projection from striate cortex to regions rostral to 19 in rhesus monkeys was reported by Zeki[59] and Cragg and Ainsworth[15]. As in the squirrel monkey[47], the lesions were confined to the representation of central vision and did not reveal an organized representation in the rostral projection zone. Spatz *et al.*[47] have related this rostral projection area in rhesus monkeys to the rostral projection area in squirrel monkey and it seems likely that at least part of the extensive, and apparently complex[60], extraoccipital projection zone in the macaque monkey will prove to be a homolog of MT.

Since little is known of the extent and organization of visual cortex in prosimians, speculation as to the possible location or existence of MT becomes difficult. There is no area of similar location and extent to area MT in the architectonic studies of tree shrews[10], lemurs[7,11], galagos[5], tarsiers[6]. But the subdivision of the posterior neocortex by architectonic methods in these primates may be incomplete and separate areas possibly have been grouped together. There is some evidence for the existence of a visual area rostral to area 19 in prosimians. Thus, in the slow loris, cortex responsive to visual stimuli extends into the region between the dorsal tip of the superior temporal sulcus and the sylvian fissure (Krishnamurti, Kaas, Wetzel, and Woolsey, unpublished investigations, see ref. 54). In tree shrews, slow-wave potentials evoked by flashes of light have been recorded over extensive regions of temporal cortex[30,35]. These fragmentary results raise the possibility that MT is an area common to all primates. However, detailed studies of the visual cortex are necessary before homologs can be ascertained with any degree of certainty.

Postulating homologies between MT and cortical areas in species more distantly related to the owl monkey becomes a hazardous procedure in view of the scarcity of information on the organization and connections of temporal visual areas. However,

some cortical regions appear promising as areas for further investigation and the possibility that area MT is part of a basic mammalian plan of neocortical organization is raised by the existence of a small temporal area adjoining peristriate cortex and caudal to auditory cortex in two primitive mammals, the hedgehog and the opossum. While there is no evidence now that this temporal region receives visual input in the hedgehog[29], a similar temporal region in the opossum[3] receives a projection from striate cortex and, thus, appears to resemble MT. Also, in the grey squirrel, a densely myelinated posterior temporal area adjoining area 19 is activated by visual stimuli[25].

However, some caution is needed in postulating homologies from the limited similarities of position, connections, or myeloarchitecture. For example, in the cat, an area lateral to area 19 responds to visual stimuli[13,27,36,57] and receives projections from striate cortex[20,26,50]. In these ways, the area is similar to MT. But, according to the architectonic studies of Otsuka and Hassler[42] and Sanides and Hoffmann[45], this lateral visual area in the cat, the Clare–Bishop visual area, does not adjoin area 19 as does MT in the owl monkey. However, this apparent difference between the Clare–Bishop area and MT may only reflect a difficulty in determining the exact lateral boundary of area 19 in the cat. A second difference between the two areas is in the manner of the representation of the visual field. A detailed comparison is not possible since the rostral-caudal organization of the Clare–Bishop area is not yet known[27], but there appears to be a clear difference in the organization of the two areas. Hubel and Wiesel[27] found that as an electrode advanced downward through the Clare–Bishop area in the medial wall of the suprasylvian sulcus, the receptive fields progressed from the temporal periphery to the vertical meridian. Such a succession of recording sites proceeds away from the striate cortex in the cat. In area MT of the owl monkey, however, receptive fields progress from the vertical meridian to the temporal periphery as the recording sites proceed rostrally away from striate cortex. Thus the progression of receptive fields in the Clare–Bishop area in the cat exhibits a reverse pattern of organization as compared to MT in the owl monkey. While the relative position of the Clare–Bishop area and the projection of the striate cortex to this area suggest the possibility of a homology between the Clare–Bishop area in the cat and MT in the owl monkey, the existing data for the visuotopic organization of the Clare–Bishop area do not support this conclusion.

We presently tend to be conservative in suggesting homologies between MT of the owl monkey and the temporal visual areas in other species. Although there is the clear possibility that MT developed early in mammalian evolution, the answer to this question must await further research. LeGros Clark[11] stressed 'the difficulty of determining whether morphological resemblances are the result of derivation from a common type or of a parallelism in evolutionary development' and suggested that this difficulty is most reliably resolved by study of the most primitive species of the group considered. To this end, it would be useful to know more of the organization and subdivision of visual cortex in prosimians. At a more basic level, further investigations on the hedgehog and opossum are needed.

SUMMARY

Visual receptive fields of single neurons and clusters of neurons were determined for recording sites in the occipital, caudal temporal and caudal parietal lobes of the owl monkey. In 7 experiments the visuotopic organization of the caudal third of the middle temporal gyrus was explored and a complete representation of the contralateral half of the visual field was revealed. This representation of the visual field (MT) corresponds to a histologically distinct area adjacent and rostral to area 19. The MT area is oval with its major axis approximately 6 mm long rostrocaudally and 4–5 mm wide mediolaterally. The horizontal meridian divides MT into a lateral portion representing the upper visual quadrant and a medial portion representing the lower quadrant. The center of gaze is represented in the caudal portion of MT bordering area 19. The representation of the periphery of the visual field lies in rostral MT immediately medial and caudal to the caudal tip of the superior temporal sulcus.

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