

Short Communications

The middle temporal visual area (MT) in the bushbaby, *Galago senegalensis*

J. M. ALLMAN, J. H. KAAS* AND R. H. LANE

Laboratory of Neurophysiology, 283 Medical Sciences Building, University of Wisconsin, Madison, Wisc. 53706 (U.S.A.)

(Accepted April 20th, 1973)

Recently we discovered a topographic representation of the visual field in the temporal cortex of the owl monkey, *Aotus trivirgatus*, which we termed the 'middle temporal visual area' (MT)¹. Such a systematic representation has not yet been demonstrated in the temporal cortex of other primates, although the probable existence of MT is indicated in several other primates by fiber connection patterns^{10-12, 15}, architectonic characteristics¹⁰, and cortical evoked potentials^{13,14}. We attempted to identify MT in the bushbaby, *Galago senegalensis*, because we wondered if this temporal visual area arose early in primate (or mammalian) evolution or was restricted to the Anthropeidea. Also, a projection from the inferior pulvinar to cortex in the expected location of MT has been demonstrated in the bushbaby^{6,7}. Since cortical projections from the pulvinar have been regarded as a major source of visual input to temporal 'association' cortex^{5,7}, it seemed important to explore the organization of this projection zone of the inferior pulvinar in the bushbaby.

The electrophysiological mapping methods used in this study were identical to those used previously for the owl monkey¹. The topography of the representation of the visual field in MT was determined by relating the positions of receptive fields for single neurons or small clusters of neurons recorded with microelectrodes to the locations of corresponding recording sites. MT was mapped in 4 adult bushbabies, which were anesthetized with urethan. Small electrolytic lesions (20 μ A for 10 sec) were made at recording sites which had receptive fields near the vertical meridian or the extreme temporal periphery of the visual field. The experimental brains were perfused with formol-saline, dehydrated, embedded in celloidin, and alternate series of 30 μ m sections were stained with thionine for cell bodies or hematoxylin for myelin (Heidenhain-Woelcke technique).

The electrophysiological and architectonic results clearly identified a region of the temporal lobe of the bushbaby as the middle temporal visual area. The location

* Present address: Department of Psychology, Vanderbilt University, Nashville, Tenn. 37240, U.S.A.

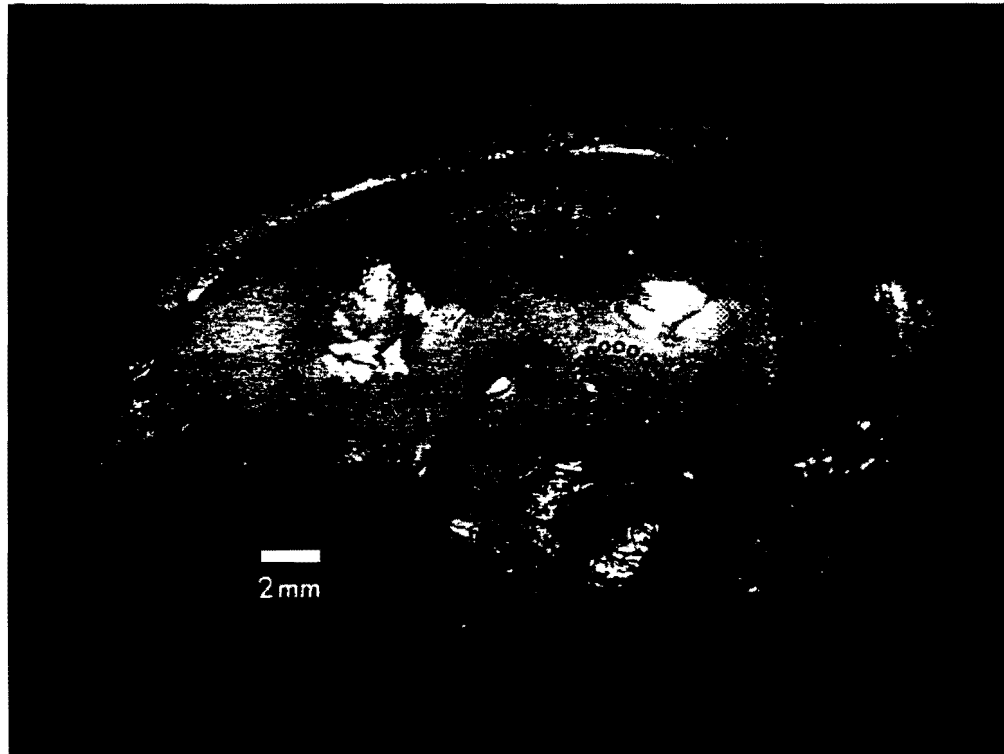


Fig. 1. The location of the middle temporal visual area (MT) in a dorsolateral view of the left hemisphere of a bushbaby. The small circles indicate the representation of the vertical meridian of the visual field, which corresponds to the border between V I and V II and also to most of the border between MT and surrounding cortex. The black triangles indicate the representation of the extreme temporal periphery of the contralateral half of the visual field, which corresponds to a portion of the rostral border of MT. The extent of V II on the dorsolateral aspect of the brain is indicated by shading.

of MT on the dorsolateral surface of the cortex is shown in Fig. 1, and the representation of the contralateral half of the visual field in MT is shown in Fig. 2. As in the owl monkey, the representation of the vertical meridian in MT of the bushbaby forms most of the border except for a small rostral segment which corresponds to the extreme temporal periphery of the contralateral half of the visual field. The horizontal meridian bisects the area into a dorsomedial portion representing the lower visual quadrant and a ventrolateral portion representing the upper visual quadrant. Central vision is represented caudally and more peripheral portions of the visual field, rostrally. In all these respects, the temporal visual area of the bushbaby and MT of the owl monkey are the same. However, proportionally less of MT is devoted to the representation of the central portion of the visual field in the bushbaby than in the owl monkey.

The organization of MT shown in Fig. 2 is based on the locations of receptive fields for 44 recording sites within the area for the single animal (72-395) illustrated.

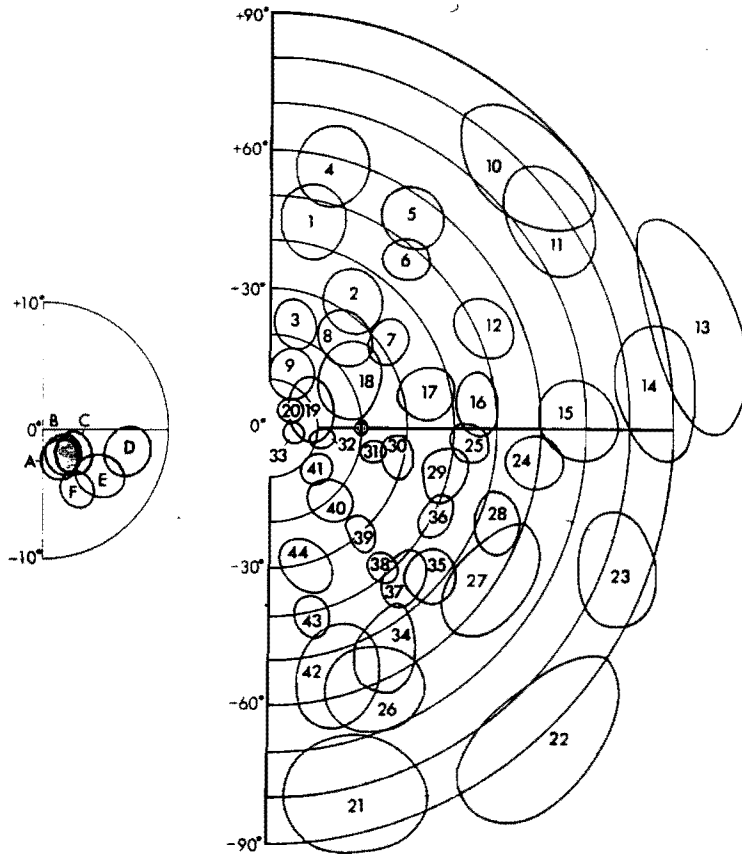
Below the dorsolateral view of the brain, an enlarged outline of MT shows the surface locations of the microelectrode penetrations for the numbered recording sites. Above the brain, the positions of the corresponding receptive fields are indicated on a perimeter chart of the contralateral half of the visual field. The results from the other bushbabies closely agreed with those illustrated for animal 72-395.

The organization of the cortex caudal to MT is similar in the bushbaby and the owl monkey. On the drawing of the brain in Fig. 2, a row of recording sites (A-F) is shown extending from the first visual area, V I, to MT. The corresponding receptive fields are shown on the small perimeter chart on the upper left indicating the central 10° of the visual field. The receptive field for the most caudal recording site (A) in V I was just below the intersection of the horizontal and vertical meridians. Receptive fields for the rostral progression of recording sites across the second visual area, V II, were successively more displaced from the vertical meridian (B, C, and D). Receptive fields for more rostral recording sites (E and F) moved back towards the vertical meridian, which forms the caudal border to MT. These results are very similar to our findings in the owl monkey which were illustrated in Fig. 8 of our earlier paper* (see ref. 1).

In the owl monkey we found that the complete representation of the contralateral half of the visual field in MT was coextensive with a densely myelinated cortical region. In brain sections stained with hematoxylin, the densely stained myelin of the deeper layers of MT clearly distinguishes MT from surrounding cortex. In adjacent sections stained with thionine, MT was identified by less dense packing of cells in cortical layer IV. In Fig. 3, similar histological features can be seen in 2 adjacent brain sections through MT in the bushbaby. The similarities of the architecture of MT in the bushbaby and the owl monkey can be seen by comparing Fig. 3 with Figs. 4, 6 and 7 in our earlier paper¹. The architecture of MT also is quite similar in the marmoset, as can be seen in the sections shown in Fig. 3 of the report by Spatz and Tigges¹⁰.

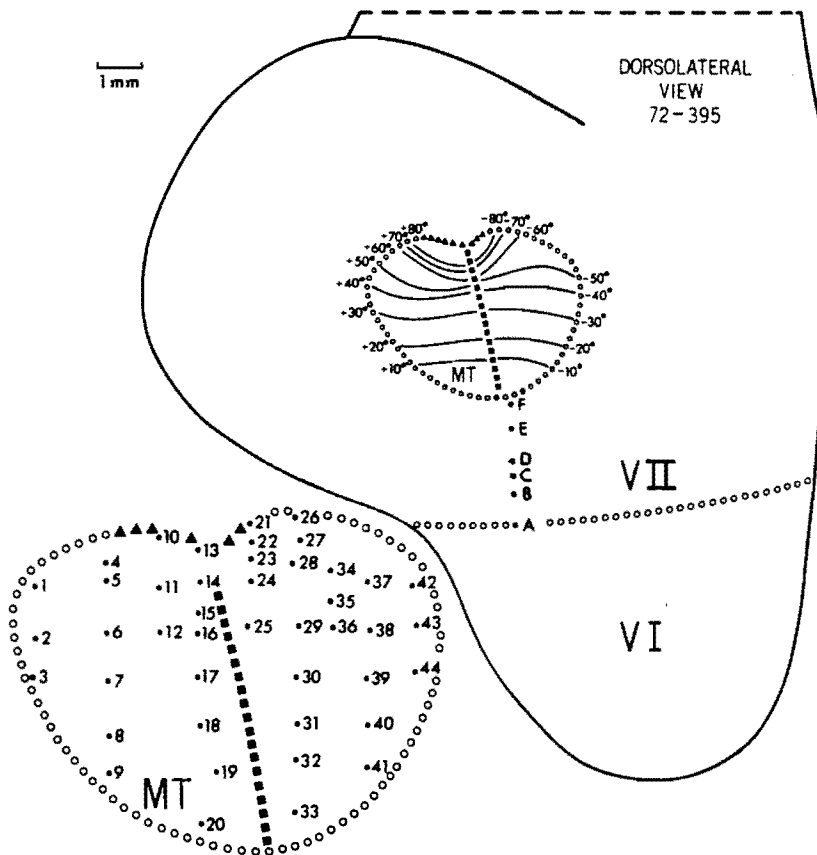
From such evidence we conclude that the middle temporal visual area (MT) is part of the visual cortex in both the owl monkey and the bushbaby. Our contention that these areas are homologous is further strengthened by the findings that V I projects to MT in New World monkeys^{10,11} and that V I also projects to the comparable region of temporal cortex in the greater bushbaby (*Galago crassicaudatus*)¹². The demonstration of MT in both New World monkeys and prosimians, along with the evidence that V I projects to a locus comparable to MT in an Old World monkey¹⁵, suggests that MT developed early in the evolution of primates or the insectivore ancestors of primates and that this area is probably basic to all primates. The existence of a non-primate homologue of MT remains uncertain. The visual cortex located on the medial bank of the suprasylvian sulcus of the cat^{4,8,9} appears to be an attractive candidate; however, Hubel and Wiesel's⁸ data indicate that the progression of receptive fields in the medial bank of the suprasylvian sulcus in the cat exhibits a reverse pattern

* Previously we considered the cortex between V II and MT as part of area 19. More extensive experiments in the owl monkey indicate that a single representation of the visual field corresponding to the classical extent of area 19 does not exist in the owl monkey^{2,3}. The cortex between V II and MT is part of a crescent-shaped representation of the visual field surrounding most of MT².



1 mm

DORSOLATERAL VIEW
72-395



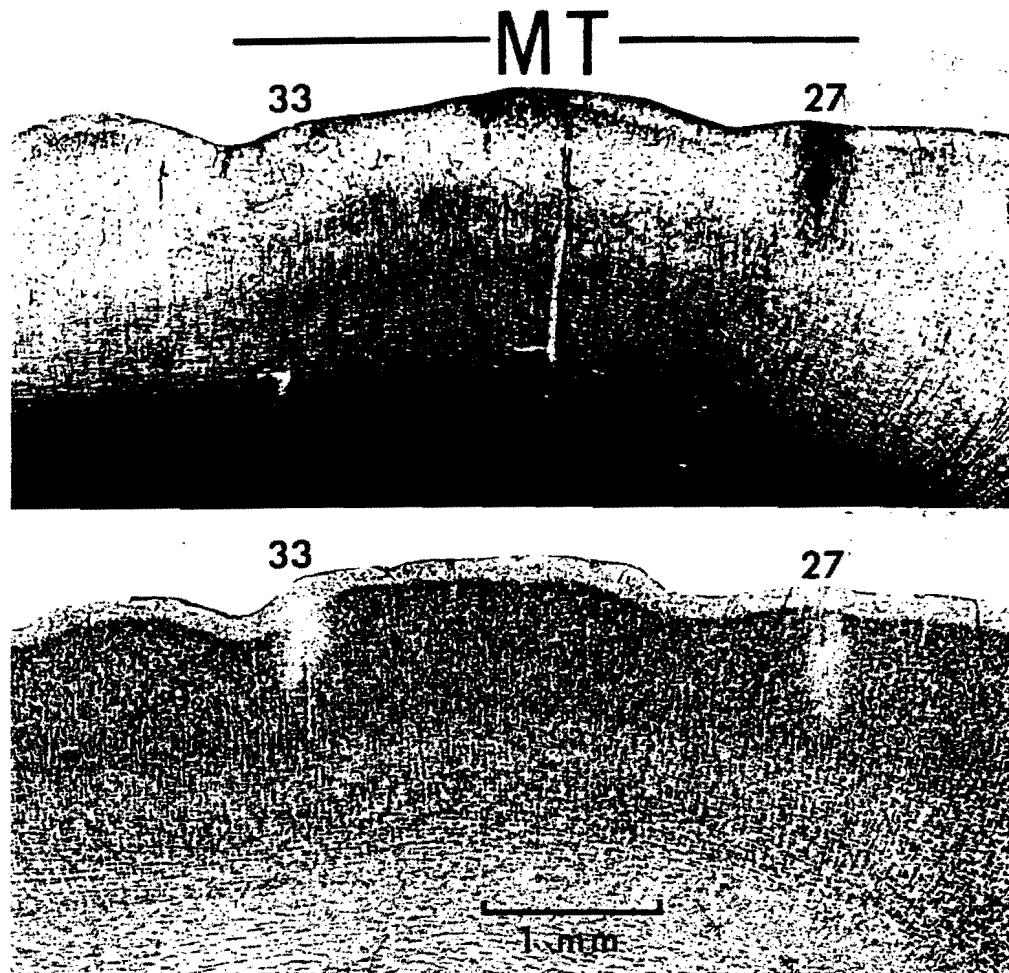


Fig. 3. Two adjacent sections illustrating the histological appearance of MT in the bushbaby. The plane of section is midway between sagittal and horizontal. The upper section was stained with hematoxylin for myelin; the lower section was stained with thionine for cell bodies. Electrolytic lesions were made at recording sites 27 and 33. Rostral is to the right.

Fig. 2. The topological transformation of the contralateral half of the visual field in MT in the bushbaby. The lower diagram is a drawing of a dorsolateral view of the caudal two-thirds of the left hemisphere. The small circles indicate the representation of the vertical meridian; the black triangles indicate the extreme temporal periphery, and the black squares indicate the horizontal meridian. The surface locations of recording sites 1-44 are shown in the enlarged view of MT, which is outlined by small circles and black triangles and lies below the drawing of the brain. Receptive fields were mapping at various depths from near the pial surface to a maximum depth of 1,350 μm . The average recording site was approximately 360 μm beneath the pial surface. The receptive fields for recording sites 1-44 in MT are illustrated in the large perimeter chart of the contralateral half of the visual field. The receptive fields for recording sites A through F in V II and the interstitial zone between V II and MT are shown in the small perimeter chart for the central 10° of the contralateral half of the visual field. The extent of V II exposed on the dorsolateral surface of the brain and the receptive fields mapped from recording sites in V II are shaded.

of visuotopic organization to that found in MT in the bushbaby and owl monkey (see refs. 1 and 13 for reviews).

The functional significance of MT is not known, but it is of interest that MT receives input from the inferior pulvinar, which in turn receives input from the superior colliculus^{6,7}. MT also receives projections from V I and perhaps other visual areas and projects to a large number of cortical and subcortical visual centers¹⁰.

We thank Dr. I. T. Diamond and Dr. W. C. Hall for providing the bushbabies, and Dr. R. W. Guillery and Dr. R. M. Benjamin for helpful comments on the manuscript. Histological materials were prepared by Mrs. I. Lucey and Mrs. J. Ekleberry. Fig. 1 was drawn by Ms. D. Urban and photographic work was done by Mr. T. P. Stewart.

Supported by NINDS Grants NS-05326 and NS-06225, NICHD Grant HD-03352, and NSF Grant GB-36779.

- 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., KAAS, J. H., LANE, R. H., AND MIEZIN, F. M., A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey (*Aotus trivirgatus*), *Anat. Rec.*, 175 (1973) 263-264.
- 3 ALLMAN, J. M., KAAS, J. H., AND MIEZIN, F. M., A dorsomedial visual area adjoining V I in the owl monkey (*Aotus trivirgatus*), *Soc. Neurosci. Abstr.*, 1 (1971) 126.
- 4 CLARE, M. H., AND BISHOP, H. G., Responses from an association area secondarily activated from optic cortex, *J. Neurophysiol.*, 17 (1954) 271-277.
- 5 DIAMOND, I. T., AND HALL, W. C., Evolution of neocortex, *Science*, (1969) 251-262.
- 6 GLENDENNING, K. K., HALL, J. A., AND HALL, W. C., The connections of the pulvinar in a primate (*Galago senegalensis*), *Anat. Rec.*, 172 (1972) 316.
- 7 HARTING, J. K., HALL, W. C., AND DIAMOND, I. T., Evolution of the pulvinar, *Brain Behav. Evol.*, 6 (1972) 424-452.
- 8 HUBEL, D. H., AND WIESEL, T. H., Visual area of the lateral suprasylvian gyrus (Clare-Bishop area) of the cat, *J. Physiol. (Lond.)*, 202 (1969) 251-260.
- 9 MARSHALL, W. H., TALBOT, S. A., AND ADES, H. W., Cortical response of the anesthetized cat to gross photic and electrical afferent stimulation, *J. Neurophysiol.*, 6 (1943) 1-15.
- 10 SPATZ, W. B., AND TIGGES, J., Experimental-anatomical studies on the "middle temporal visual area (MT)" in primates. I. Efferent cortico-cortical connections in the marmoset (*Callithrix jacchus*), *J. comp. Neurol.*, 146 (1972) 451-463.
- 11 SPATZ, W. B., TIGGES, J., AND TIGGES, M., Subcortical projections, cortical associations, and some intrinsic interlaminar connections of the striate cortex in the squirrel monkey (*Saimiri*), *J. comp. Neurol.*, 140 (1970) 155-173.
- 12 TIGGES, J., TIGGES, M., AND KALAH, C., Efferent connections of area 17 in *Galago*, *Amer. J. Physical Anthropology*, 38 (1973) 393-398.
- 13 WOOLSEY, C. N., Comparative studies of cortical representation of vision, *Vision Res.*, Suppl. 3 (1971) 365-382.
- 14 WOOLSEY, C. N., AKERT, K., BENJAMIN, R. M., LEIBOWITZ, H., AND WELKER, W. I., Visual cortex of the marmoset, *Fed. Proc.*, 14 (1955) 166.
- 15 ZEKI, S. M., Representation of central visual fields in prestriate cortex of monkey, *Brain Research*, 14 (1969) 271-291.